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Cytotaxonomy of Antarctic teleosts of the *Pagothenia/Trematomus* complex (Nototheniidae, Perciformes)

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Summary. The interspecific relationships and taxonomy of 12 antarctic coastal Nototheniids (the *Pagothenia/Trematomus* complex) are still under discussion. Here we present karyological data on eight species in hope that further cytogenetic data can help to clarify phylogenetic problems. *Pagothenia bernacchii* ($2n=48$) has a generalized karyotype which has not developed heterochromosomes. *P. hansoni*, *P. borchgrevinki* and *Trematomus newnesi* share very similar karyotypes with $2n=46$ for females and $2n=45$ for males. The difference between sexes is probably due to the development of a multiple sex-chromosome system with a neo-Y, typical of males, which originated from a centric fusion of an autosome (now X_2) with an undifferentiated Y. The chromosome morphology of the three species seems to be related to that of *P. bernacchii*. *T. nicolai* ($2n=58$, 57) has a karyotype numerically and morphologically divergent from that of the above species; *T. nicolai* males may have developed a neo-Y through a tandem translocation. *T. pennellii* ($2n=32$), *T. loennbergii* ($2n=28$; $2n=30$ in a single female) and *T. eulepidotus* ($2n=24$) show karyotypes with progressively fewer chromosomes but with an increasing number of large, bi-armed chromosomes. Such a "symmetrization" process is generally found in advanced poikilothermic Vertebrates and the three species of *Trematomus* could therefore be considered as karyologically derived. However, parallelism in the karyotype differentiation producing convergence in the chromosome morphology of distantly related species cannot yet be excluded.

Introduction

With about 50 species mostly endemic to the Southern Ocean, the *Nototheniidae* (suborder *Notothenioidei*, *Perciformes*) are the most ecologically diverse group of antarctic Teleosts (Andriashev 1965; DeWitt 1971; Andersen 1984; Clarke 1988; Eastman 1991). Twelve benthic or benthopelagic species of this family are considered strictly related on morphological grounds and hence classified either in a single subfamily *Trematominae* (Balushkin 1982), or in a single tribe *Pagotheniini* (Andersen 1984). However, the intra- and intergeneric relationships of this group of species (here called the *Pagothenia/Trematomus* complex) are still debated and recently at least three different classifications have been proposed.

All authors agree that the widehead cryopelagic species *brachysoma* and *borchgrevinki* should be assigned to the genus *Pagothenia* (DeWitt 1964; Andriashev and Jakubowski 1971). Balushkin (1982, 1984) places the species *newnesi* in the genus *Trematomus* and establishes a new genus *Pseudotrematomus* for a group of ten species (*bernacchii, eulepidotus, hansoni, lepidorhinus, loennbergii, nicolai, pennellii, scotti, tokarevi* and *vicarius*). DeWitt et al. (1990) do not find sufficient reason to admit two different genera and place all three species, and *newnesi*, in the same genus *Trematomus*. Andersen (1984), here followed by Hureau (1985) but criticized by DeWitt et al. (1990), gives weight to the common presence of cephalic pit lines in five species (besides *brachysoma* and *borchgrevinki, bernacchii, hansoni* and *tokarevi*) and groups these taxa in the genus *Pagothenia*, while the remaining species compose the genus *Trematomus*.

In order to contribute to the natural history of coastal Nototheniids, we have collected karyological data on eight species of the *Pagothenia/Trematomus* complex (*bernacchii, borchgrevinki, eulepidotus, hansoni, loennbergii, newnesi, nicolai* and *pennellii*) using *Notothenia coriiceps* (*Nototheniinae*) as an outgroup. Chromosome differentiation may be independent from other morphological traits and has often proved useful in making phylogenetic reconstructions (White 1973).

Material and methods

In the course of the 1989/90 and 1990/91 campaigns of the Italian National Program for Antarctic Research (PNRA), specimens of various notothenioid species were fished by one of us (E.P.) in Terra Nova Bay (Ross Sea), near the Terra Nova Italian antarctic base (74°41′42″ South, 164°07′23″ East); Dr. A.L. De Vries kindly provided us with four specimens of *P. borchgrevinki* from Mc Murdo U.S. base.

We have obtained chromosomes from the following specimens (for convenience, we use the classification of Hureau, 1985, which was

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also used to identify the animals in the field):

- *Pagothenia* (*Trematomus*) bernacchii (Boulenger 1902): five males, eleven females;
- *Pagothenia borchgrevinki* (Boulenger 1902): two males, two females;
- *Pagothenia* (*Trematomus*) hansoni (Boulenger 1902): three males, ten females;
- *Trematomus eulepidotus* Regan 1914: one male, three females;
- *Trematomus loennbergii* Regan 1913: three males, two females;
- *Trematomus newnesi* Boulenger 1902: seven males, one female;
- *Trematomus nicolai* (Boulenger 1902): one male, one female;
- *Trematomus pennellii* (= *centronotus*) Regan 1914: four males, three females;
- *Notothenia coriiceps* Richardson 1844: one male.

These specimens have been deposited in the ichthyological collect at the Museum of the Institute of Comparative Anatomy, University of Genoa, and in the antarctic collections of the ICRAP, Rome.

Living fish received a dose of colchicine and were sacrified from four to twelve hours later; kidney and spleen cells were collected using the techniques described by Doussau de Bazignan and Ozouf-Costaz (1985). Slides with fixed cells were stained with Giemsa in loco; other fixed material was sent to Italy for more elaborate staining techniques, i.e. C-banding and NOR-banding to localize respectively the main heterochromatic fractions and the nucleolus organizer regions (NORs) (for details, cf. Schmid et al. 1990). Karyotypes were obtained from metaphasic plates of both sexes in each species, except *N. coriiceps*. Conventionally, when karyotyping the bi-armed chromosomes (metacentric: MC; submetacentric: SM; subtelocentric: ST) have been placed before the uniarmed chromosomes (acrocentric: AC); characterization of chromosome morphology follows Levan et al. (1964).

Results

The diploid chromosome number (2n), karyotype composition in MC, SM, ST or AC chromosomes, number of chromosome arms (FN = fundamental number), the presence (if any) of a multiple sex chromosome system X_1YX_2 in the male specimens, are summarized in the Table 1 for all studied species. Chromosome material was abundant in each species probably because cell division is very active in kidney and spleen during the short austral summer when specimens were caught. Each species had a constant karyotype, except for sex-linked heteromorphism in four species and the karyotype of *T. loennbergii*, where two diploid numbers were found: 28 chromosomes (karyomorph A, in three males and one female) and 30 chromosomes (karyomorph B, in one female).

In *P. bernacchii* ($2n = 48$) male and female specimens showed the same karyotype morphology: two pairs of small, bi-armed chromosomes (pair 2 is submetacentric and carries well developed, sometimes heteromorphic in length, NORs on the shorter arms) and 22 pairs of acrocentric chromosomes of regularly decreasing size (pairs 3–24). C-banding localized heterochromatic areas on the centromeres of nearly all pairs and on the telomeres of some pairs; in the case that sex genes are preferentially located on a single pair of gonosomes, they exhibit the same morphology in both sexes (Fig. 1A).

P. hansoni, *P. borchgrevinki* and *T. newnesi* showed very similar karyotypes both in females ($2n = 46$) and in males ($2n = 45$). Females have three pairs of bi-armed chromosomes (pair 1 is a large, metacentric element; pairs 2 and 3 are equal to pairs 1 and 2 of *P. bernacchii*, pair 3 carries NORs) and 20 pairs of acrocentric chromosomes of decreasing size (two of these pairs may be sex chromosomes). Males of the three species have two fewer acrocentric chromosomes, but one very large, unpaired metacentric chromosome not present in females.

Using White's (1973) terminology for multiple heterochromosomes, the monosomic metacentric of the male is a neo-Y sex chromosome that may be derived from a centric fusion of two acrocentric elements (the two missing in the male but present in the female karyotype). This fusion has involved an acrocentric, simple Y chromosome morphologically undifferentiated from X, and an acrocentric autosome now sex-linked in the male sex (X_2), while the original X now can be called X_1 (Fig. 2).

In conclusion, *P. hansoni*, *P. borchgrevinki* and *T. newnesi* have a karyotype constituted by 21 autosome pairs and a multiple sex-chromosome system that is X_1YX_2 in the male ($2n = 45$) and $X_1X_1X_2X_2$ in the female ($2n = 46$) (Fig. 1B/D).

Possibly sex-linked differences have also been found in the karyotypes of the two specimens of *T. nicolai*. The female ($2n = 58$) has 4 pairs of meta- and submetacentric chromosomes, 9 pairs of subtelocentric chromosomes and 16 pairs of acrocentric chromosomes. The NORs are located on the short arms of a small submetacentric pair that is morphologically very similar to the corresponding NOR bearing chromosomes of previously studied species of this complex. The male ($2n = 57$) shows one large, metacentric chromosome (possibly the derived Y) not seen in females, and two unpaired chromosomes – one acrocentric, the other submetacentric – which in the female are regularly present in pairs. We suggest that these two chromosomes are the X_1 and the X_2 elements whose partners are fused in the multiple Y. The fusion of both chromosomes most probably occurred by a tandem translocation (Fig. 1E).

If the early, ancestral Y of *T. nicolai* predecessors was similar to that observed in other nototheniids, then the X_1 may be an acrocentric, and the X_2 a submetacentric.

In *T. pennellii* ($2n = 32$) male and female specimens show the same karyotype morphology. The acrocentric pairs are reduced to 9 and the remaining chromosomes are meta- or submetacentric; NORs are again localized on a small pair of elements similar to that of other species of the complex (Fig. 3F).

Four of the 5 specimens of *T. loennbergii* (three males, one female) show $2n = 28$ and a karyotype made up of 12 pairs of bi-armed, meta- or submetacentric chromosomes and 2 pairs of small acrocentric chromosomes; as usual, the NORs are located on a small pair of submetacentric elements. No sex-linked differences have been found in this 28-chromosome karyotype, here indicated as *karyomorph* A (Fig. 3G).

A second female of *T. loennbergii* has $2n = 30$ and its karyotype differs from that of the other co-specific specimens in lacking one pair of metacentric chromosomes and in having two extra pairs of acrocentrics (*karyomorph* B; Fig. 3H). Since both karyomorphs show the same number of chromosome arms (NF), their relationships could be Robertsonian (White 1973), i.e. one of the two is derived from the other through a centric fusion (from 30 to 28) or fission (from 28 to 30). Given the small sample of specimens, it is not possible to make definitive conclusions.

T. eulepidotus ($2n = 24$) has all bi-armed chromosomes ($NF = 48$) which are of relatively large size except a pair of small submetacentric elements carrying the NORs on the short arms; no sex differences in karyotypes were found (Fig. 3L).

The single specimen of *N. coriiceps* has 22 bi-armed chromosomes; in this species the NORs are located on a pair of metacentric chromosomes which are the largest chromosomes in the karyotype (Fig. 3M).

Discussion

Prirodina and Neyelov (1984), Phan et al. (1986), Ozouf-Costaz and Doussau de Bazignan (1987) have described the karyotypes of some of the species studied by us. Our results on *N. coriiceps* ($2n = 22$) confirm those obtained by Prirodina and Neyelov (1984) on specimens from South Shetlands. Phan et al. (1986) found $2n = 48$ in specimens of *P. bernacchi* and *P. hansoni* (one for each species) from South Shetlands: since our specimens of *P. hansoni* have 46 or 45 chromosomes depending upon sex, this discrepancy (if the specimen from South Shetland is representative of the whole local population) could depend on a chromosome polymorphism inside *P. hansoni* (such polymorphism is not new in Perciforms; cf. Thode et al. 1985).

Ozouf-Costaz and Doussau de Bazignan (1987) found $2n = 24$ in specimens of *T. eulepidotus* from Prydz Bay. Our specimens show the same diploid number, but all their chromosome pairs are bi-armed, while animals from Prydz Bay have one pair of long acrocentric chromosomes.

A karyotype composed by 48 acrocentric chromosomes seems to be common in Teleosts, many orders of which – including Perciforms – contain species which share this diploid number that is generally considered primitive for bony fishes (Ohno 1974; Gold 1979; Sola et al. 1981; Ojima 1983). Although this may be considered a working hypothesis, in other poikilothermic Vertebrates (Amphibians) commonly shared karyotypes are more often interpreted as the product of convergence (Morescalchi 1975, 1990).

If we start from the assumption that a 48-chromosome karyotype is plesiomorphic in Perciforms (and also in Nototheniids; cf. Prirodina 1986; Ozouf-Costaz and Doussau de Bazignan 1987), then *P. bernacchii* could have the most primitive karyotype among the species studied here, even though it has two pairs of small, bi-armed elements. However, these last chromosomes appear to be very conservative (especially those with NORs), because they are present in the karyotypes of nearly all the species of the *Pagothenia*/*Trematomus* complex. These small bi-armed chromosomes seem to be also present in the karyotype of a single studied female of *T. lepidorhinus* who has $2n = 48$ and a formula very similar to that of *P. bernacchii* (Ozouf-Costaz and Doussau de Bazignan 1987). Even *Dissostichus eleginoides*, from a genus considered ancestral for Nototheniids (Andersen 1984), has 48 chromosomes which all are acrocentric except two pairs of small bi-armed elements. Our results could be considered as a further indication that this formula is ancestral for Nototheniids in agreement with the conclusions of Ozouf-Costaz and Doussau de Bazignan (1987).

Relationships between a 48-chromosome karyotype (such as that of *P. bernacchii*) and a 46-chromosome karyotype of the type shared by *P. hansoni*, *P. borchgrevinki* and *T. newnesi* (female sex), can be easily traced: a single chromosome rearrangement, such as a centric fusion, may have changed a 48 chromosome karyotype to one with 46 (or vice-versa if a centric fission is postulated). A further centric fusion may explain – as we have said – the rise of a multiple Y and that of an odd chromosome number ($2n = 45$) in the males of *P. hansoni*, *P. borchgrevinki* and *T. newnesi*. This interpretation is in favour of the origin of the 46-chromosome karyotype from that with 48 chromosomes, because *P. bernacchii* ($2n = 48$) does not have heteromorphic sex chromosomes in the male.

P. hansoni, *P. borchgrevinki* and *T. newnesi* share the same karyotype model in both females ($2n = 46$) and males ($2n = 45$). The males exhibit an elaborate sex chromosome system that can be considered an apomorphic character (Ojima 1983). Thus, from a karyological standpoint, the three species appear strictly related even if more than one species (*P. bernacchii*, *T. lepidorhinus*) has the (presumably) ancestral karyotype composed of 48 chromosomes, suggesting that the 46/45 chromosome karyotype could have

Table 1. The main karyotype characters of the studied Nototheniidae

	2n	MC	SM	ST	AC	FN	X_1YX_2
P. bernacchii F/M	48	2	2		44	52	no
P. hansoni F/M	46/45	4	2		40	52	yes
P. borchgrevinki F/M	46/45	4	2		40	52	yes
T. newnesi F/M	46/45	4	2		40	52	yes
T. nicolai F/M	58/57	2	6	18	32	84	yes
T. pennellii F/M	32	12	2		18	46	no
T. loennbergii (A) F/M	28	18	6		4	52	no
T. loennbergii (B) F	30	16	6		8	52	?
T. eulepidotus F/M	24	22	2			48	no
N. coriiceps M	22	18	4			44	no(?)

2n: diploid number; MC–SM–ST–AC: metacentric, submetacentric, subtelocentric and acrocentric chromosomes; FN: fundamental number; X_1YX_2: presence of a multiple Y sex chromosome. F/M: female and (or) male specimens

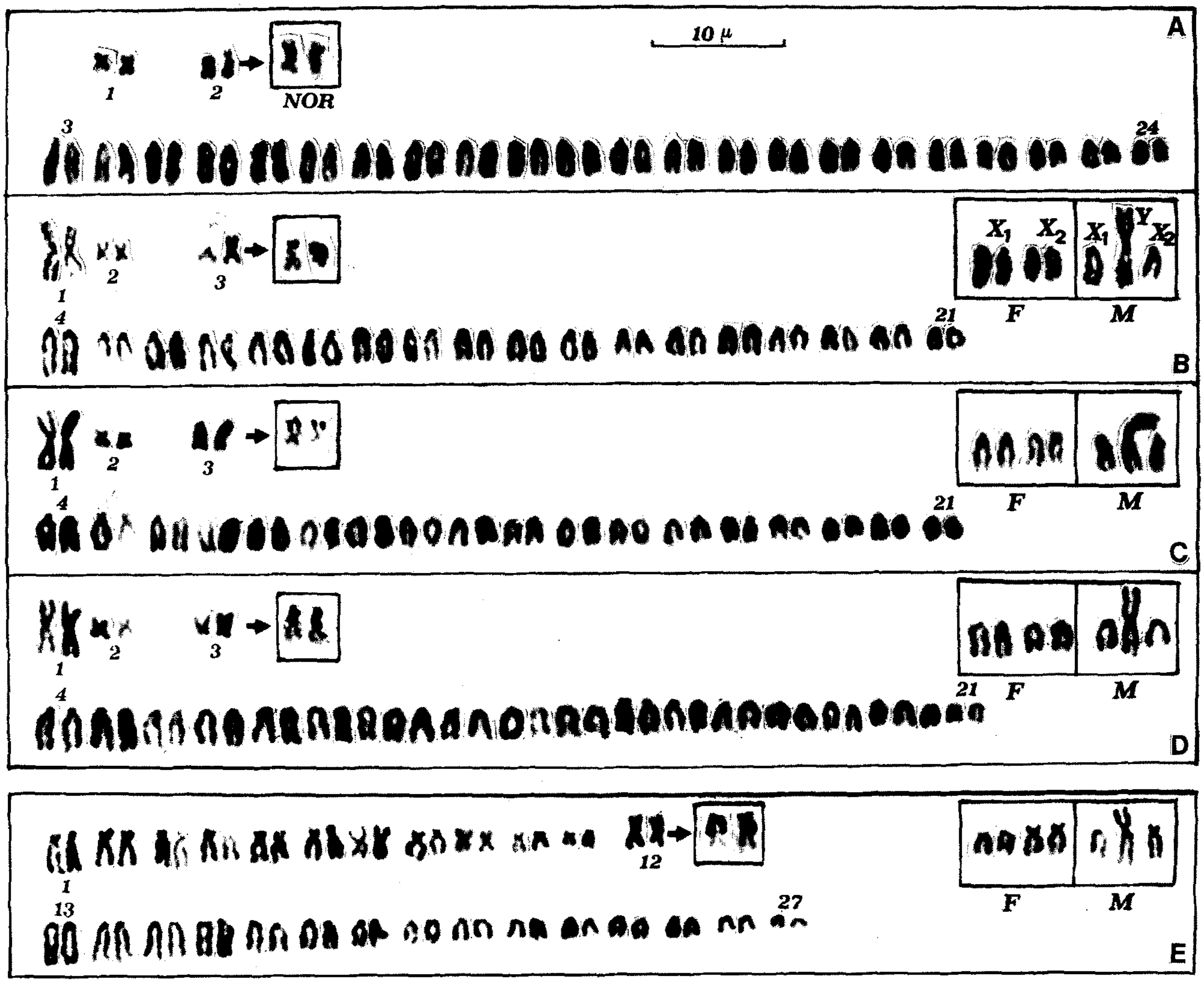

Fig. 1. The karyotypes of *P. bernacchii* (*A*), *P. hansoni* (*B*), *P. borchgrevinki* (*C*), *T. newnesi* (*D*) and *T. nicolai* (*E*), all at the same enlargement (*bar*). The chromosome pair carrying nucleolar organizers is represented twice, after Giemsa staining (*arrow origin*) and after silver nitrate staining (*NOR, framed*). When multiple sex-chromosomes are present (in *B,C,D* and *E*) they can be found framed on the right side of the figure and apart the commonly shared autosomes (*F*: sex chromosomes of female, $X_1X_1X_2X_2$; *M*: sex chromosomes of male, X_1YX_2)

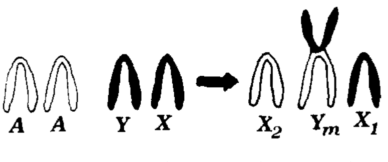

Fig. 2. Origin of the multiple sex chromosomes in the male of the species with 46/45 chromosomes: the neo-Y (Y_m) can be derived from the centric fusion of an autosome (*A*) with an early *Y* morphologically indifferentiated from the *X*. The neo-Y of *T. nicolai* can be derived from a tandem translocation

been evolved in parallel among different species. Indeed, the Robertsonian mechanisms involving centric fusion or fission seem to be rather common in bony fishes and, in species belonging to some Perciform families, can also produce chromosome polymorphism (Thode et al. 1985; Vitturi and Catalano 1988, 1989).

The karyotype of *T. nicolai* (2n = 58/57), both in terms of the high chromosome number and in the presence of many subtelocentric chromosomes, appears the most divergent among the species of the *Pagothenia*/*Trematomus* complex and also among other studied Nototheniids (cf. Ozouf-Costaz and Doussau de Bazignan 1987). If the two specimens analyzed here are representative, a multiple sex-chromosome system has evolved independently in *T. nicolai*. The neo-Y of *T. nicolai* seems to have arisen from the tandem translocation of an acrocentric element (perhaps the ancestral Y) to the short arm of a submetacentric chromosome (the X_2?) with a mechanism new for Nototheniids but also found in a related family, the Channichthyids, (some species of the genus *Chionodraco*; cf. Morescalchi et al. 1992).

While reinforcing the hypotheses of parallelism in the evolution of sex chromosomes among Notothenioids (or in all Perciforms, given that a neo-Y has been described in

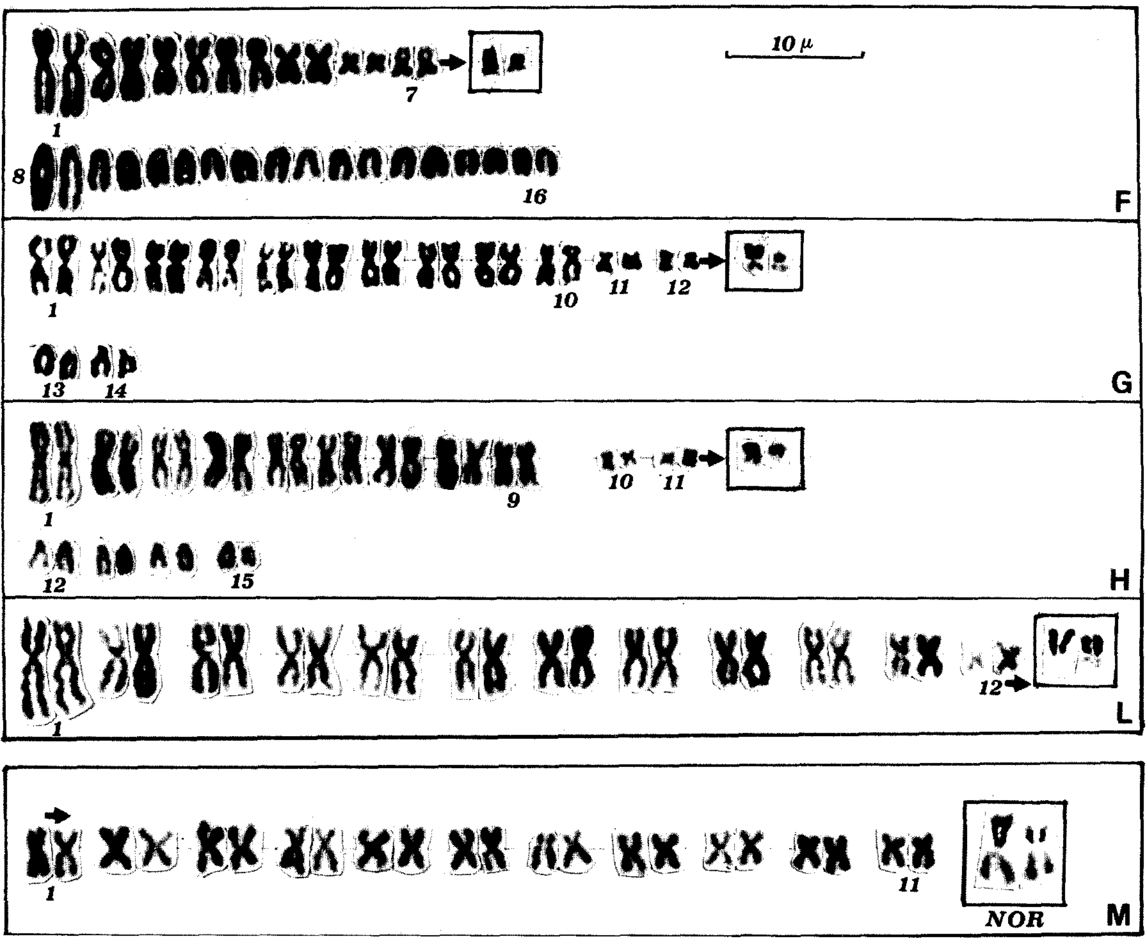

Fig. 3. The karyotypes of *T. pennellii* (*F*), *T. loennbergii* karyomorph A (*G*) and karyomorph B (*H*), *T. eulepidotus* (*L*) and *N. coriiceps* (*M*), all at the same enlargement (*bar*)

Blenniids by Carbone et al. 1987), this result also supports Ohno's theory (1974) on the indifferentiated condition of fish gonosomes, which may still contain a large number of autosomal genes (see also Kallman 1984; Nanda et al. 1990).

Trematomus pennellii (2n = 32), *T. loennbergii* (2n = 28, 30) and *T. eulepidotus* (2n = 24) do not have heteromorphic sex chromosomes and show many more bi-armed chromosomes than the other species of the complex. The bi-armed chromosomes increase as the diploid number decreases. Since the FN does not show much variation, the increase of bi-armed chromosomes, if lower diploid numbers are derived, is probably Robertsonian, i.e. due to fusion (Ohno 1974; Ojima 1983).

Indeed, a tendency towards karyotypic "symmetrization" (diploid sets constituted entirely by bi-armed chromosomes) seems to be common in both plants and animals (Stebbins 1966; White 1973) and has been discussed for poikilothermic Vertebrates such as Amphibians and Teleosts (Morescalchi 1975, 1990; Garcia et al. 1987). Adopting this hypothesis, *T. pennellii*, *T. loennbergii* and *T. eulepidotus* could be placed along a gradient of karyotype differentiation from "asymmetrical" and numerically elevated karyotypes (2n = 48 with the most acrocentric elements) to "symmetrical" and reduced karyotypes mostly constituted by meta- or submetacentric elements.

This trend is not unique to the species of the *Pagothenia/Trematomus* complex and may be present in other Nototheniids (Prirodina 1986; Ozouf-Costaz and Doussau de Bazignan 1987). For example, *N. coriiceps* (Nototheniines) has a typically symmetrized (i.e. evolved) karyotype (2n = 22, all with bi-armed elements).

In conclusion, from a karyological point of view, the species of the *Pagothenia/Trematomus* complex studied here can be divided into three groups.

One karyological group includes the species with 46/45, mostly acrocentric, chromosomes and with a multiple sex chromosome system, i.e. *P. hansoni*, *P. borchgrevinki* and *T. newnesi*; *P. bernacchii* can be added to this group as representative of a somewhat more generalized karyological condition. The second group includes only *T. nicolai* (2n = 58/57) whose karyological relationships with other species of the complex are not well known. The third group includes species with progressively symmetrized karyotypes (*T. pennellii*, *T. loennbergii* and *T. eulepidotus* in the order) which probably represent a more advanced (but not necessarily monophyletic) condition in comparison with the species of the first group.

However, the various possibilities of chromosomal coevolution suggest caution in relying solely on karyological data for making taxonomic decisions. Data on genome size, GC-content and satellite DNA would be useful and is programmed by our group. Clearly, all such data should be integrated with other biological information such as DNA sequences and morphology to provide a more complete evolutionary reconstruction.

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