Several possible mechanisms might explain blue-light reversibility in *Daphnia*. The most obvious possibility is the presence of a photochromic molecule analogous to phytochrome⁶. Equally plausible is the modification of a photosensitive molecule within an electron transport chain²³. The least likely possibility is a long day/short day alternative reaction¹⁰, although the blue light receptor could be involved in a photoperiodic mechanism. The photoreversal mechanism in *Daphnia* appears to be distinct from well known photoperiodic reactions in other animals since it is

independent of daylength, sensitive to low fluence rates, and transitory.

A photoreversible reaction, such as exists in *Daphnia*, is likely to be found in other arthropods, and indeed in all organisms known to be sensitive to blue light. The search for similar blue light-reversible reactions in other animal systems will prove very exciting and will greatly aid in understanding the relevance of such reactions.

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- 1 Borthwick, H. A., Hendricks, S. B., Parker, M. W., Toole, E. H., and Toole, V. K.,, Proc. natn. Acad. Sci. USA 38 (1952) 662.
- 2 Kumagai, T., and Bjorn, L.O., Physiologia Pi. 60 (1984) 449.
- 3 Löser, G., and Schäfer, E., in: The Blue Light Syndrome, p. 244. Ed. H. Senger. Springer-Verlag, Berlin 1980.
- 4 Erlanger, B. F., and Wassermann, N. H., in: Trends in Photobiology, p. 81. Eds C. Hélène, M. Charlier, Th. Montenay-Garestier and G. Laustriat. Plenum Press, New York 1982.
- 5 Smith, H., Symp. Soc. expl Biol. 36 (1983) 81.
- 6 Smith, H., Phytochrome and Photomorphogenesis. McGraw-Hill, Maidenhead 1975.
- 7 Hendricks, S. B., Proc. natn. Acad. Sci. USA 58 (1967) 2125.
- 8 Kumagai, T., Physiologia Pl. 57 (1983) 468.
- 9 Kumagai, T., Physiologia Pl. 59 (1983) 590.
- 10 Lees, A.D., J. Insect Physiol. 27 (1981) 761.
- 11 Klemm, E., and Ninnemann, H., Photochem. Photobiol. 24 (1976)

- 12 Danilevskii, A.S., Photoperiodism and Seasonal Development in Insects. Oliver and Boyd, London 1965.
- 13 Saunders, D.S., An Introduction to Biological Rhythms. J. Wiley and Sons, New York 1977.
- 14 Pancella, J.C., and Stross, R.G., Chesapeake Sci. 4 (1963) 135.
- 15 Stross, R. G., Ecology 47 (1966) 368.
- 16 Davison, J., J. gen. Physiol. 53 (1969) 562.
- 17 Stross, R.G., unpublished.
- 18 Davison, E. A. Jr, A Blue Light-Reversible Photoresponse Controlling Embryonic Development in Daphnia pulex. Thesis, Library State Univ. at Albany, New York 1984.
- 19 Sokal, R., and Rohlf, J., Biometry, 2nd edn. W. H. Freeman and Co., San Francisco 1981.
- 20 Ninnemann, H., Bioscience 30 (1980) 166.
- 21 deFabo, E., Harding, R. W., and Shropshire, W. Jr., Pl. Physiol. 57 (1976) 440.
- 22 Muñoz, V., and Butler, W. L., Pl. Physiol. 55 (1975) 421.
- 23 Kumagai, T., Photochem. Photobiol. 27 (1978) 371.

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Karyological conservatism in South American camelids^{1,2}

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Summary. Llama, guanaco, vicuna and alpaca show similar diploid numbers, gross chromosomal morphology and homologous G, C and NOR banding patterns. This chromosomal homology is also found in the two-humped camel and very probably in the one-humped camel as well. These findings indicate that the camelid karyotype can probably be traced back to early Miocene times. This probably represents the most extreme case of chromosomal conservatism among mammals.

Key words. Karyological conservatism; camelids; camelids karyology.

Taylor et al. in 1968³ described similar diploid numbers and gross chromosome morphology for *Lama glama* (llama), *Camelus bactrianus* (two-humped camel) and *C. dromedarius* (one-humped camel). In 1983 Larramendy et al.⁴ reported that *L. guanicoe* (guanaco) and *L. glama* showed a complete homology of G banding patterns. This homology was recently confirmed by Bunch et al.⁵ who also extend the studies to *C. bactrianus* and to C- and NOR banding patterns.

In this report we present information on G, C and NOR banding patterns for the four species forming the group of South American camelids. Our data show the presence of a complete karyological conservatism for L. guanicoe, L. glama, L. pacos (alpaca) and L. vicugna (vicuna).

Material and methods. A total of two llamas, four guanacos, three vicunas and three alpacas were studied. Sex and origin of animals was as follows: llama, one male and one female from La Plata Zoo; guanaco, three males from La Plata Zoo and one female from the reserve of Trelew, Province of Chubut (Argentina); vicuna and alpaca, one male and two females from the reserve of Abra Pampa, Province of Jujuy (Argentina).

Blood cultures were set up according to Halman⁶. Culture medium contained 20% of fetal calf serum and was supplemented with L-cysteine 0.02%, L-glutamine 0.01% and L-tyrosine

0.03%. Harvesting was performed at 72 h. Colchicine treatments (0.1 µg/ml) lasted 3 h. Chromosome spreads were obtained by air drying.

C-banding was induced with the BaOH technique of Sumner⁷. Trypsin digestion was employed for G banding⁷. The silver method was used for identification of NOR⁹.

A total of five to ten karyotypes per animal and per cytogenetic method were employed for karyological characterization of each species.

Results. Modal chromosome number in the four species was 2n = 74. The four species also showed similar chromosome morphology and similar NOR, C and G banding patterns.

According to gross morphology the autosomal pairs were arranged in two groups and within each group by order of decreasing size. Pairs 1–20 were acrocentric-subterminal; pairs 21–36 metacentric-submetacentric. X chromosomes were the longest metacentric of the set, while the Y chromosome was the smallest acrocentric. Pairs 1 and 18 could also be identified with accuracy on morphological grounds. Chromosomes 1 were the longest subterminal elements in the complement; pair 18 showed a constant and marked secondary constriction in the short arm producing the appearance of satellites.

All chromosomes showed positive C banding. Pairs 22-25 and

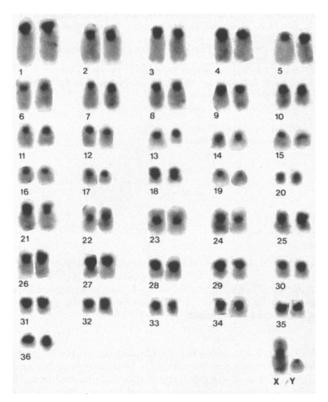


Figure 1. C-band pattern of a male guanaco. The other three species have the same C-band distribution.



Figure 2. Metaphase of a female guanaco. Nucleolar organizing chromosomes are arrowed. The other three species show the same pattern.

the X chromosome exhibited C banding restricted to the centromere regions; pairs 19, 20 and the Y chromosome showed very small and poorly defined centromere bands. All other pairs had conspicuous C bands comprising the centromere region and the whole short arm (fig. 1).

The number of chromosomes with positive NOR varied from four to six (two to three pairs). NOR regions corresponded to the secondary constriction of pair 18 and the short arms of pair



Figure 3. Comparative G-band patterns of guanaco (G), llama (L), alpaca (A) and vicuña (V). The same species order is used for each chromosome group.

27, and less frequently of pair 21 (tentative identification) (fig. 2). Figure 3 illustrates the complete homology of G banding patterns in the four species.

Discussion. This and previous reports point out a complete karyological homology for the two-humped camel, guanaco, llama, alpaca and vicuna^{4,5}. Since the one-humped camel has the same diploid number and gross chromosomal morphology as the other three species³ it also seems logical to expect a G, C and NOR banding homology for this species as well.

For most of the 40-45 million years of its evolution, the camel family was entirely a North American group; Protylopus petersoni being the earliest camel identified. Fossil records indicate that the extinct genus Procamelus of the early Miocene epoch shows similarities to present day *Camelus* and *Lama* and may have been ancestral to both 10,11. Therefore, the chromosome complement of modern camelids may perhaps be traced back to Procamelus indicating a complete chromosomal stability for approximately 15-25 million years. Although karyotypes from humans and big apes have also shown a marked stability for about 20 million years, there are some interspecies chromosomal rearrangements and variations in the amount and distribution of C bands in this taxon^{12,13}. Thus, the camelid karyotype seems to be the most extreme case of karyological conservatism thus far known among mammals. In South American camelids, the karyotype conservation is coincident with remarkable phenotype similarities and also with the well-documented cases of interspecies hybridizations with production of fertile hybrids¹⁴.

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- Taylor, K.M., Hungerford, D.A., Snyder, R.L., and Ulmer, F.A. Jr, Cytogenetics 7 (1968) 8.
- Larramendy, M. L., Vidal-Rioja, L., Bianchi, M. S., and Bianchi, N.O., Proc. IX Latin Am. Cong. Zool. 159 (1983).
- Bunch, T.D., Foote, W.C., and Maciulis, A., J. Hered. 76 (1985)
- Halman, C. R. E., Res. Vet. Sci. 22 (1977) 40.
- Sumner, A.T., Exp. Cell Res. 75 (1972) 304.
- Wang, H.C., and Fedoroff, S., Nature New Biol. 235 (1972) 52.
- Goodpasture, C., and Bloom, S. E., Chromosoma 53 (1975) 37.
- Webb, S.D., in: Pleistocene Mammals of Florida, p. 170. Ed. S.D. Webb. University Press of Florida, Gainsville 1974.
- Franklin, W.L., in: Mammalian Biology in South America, p. 457. Eds M.A. Mares and H.H. Genoways. University of Pittsburgh, Pittsburgh 1981.
- Seuanez, H.H., The Phylogeny of Human Chromosomes. Springer-Verlag, Berlin 1979.
- Yunis, J.J., and Prakash, O.M., Science 215 (1982) 1525.
- 14 Romero, E. C., Llamas, alpacas, vicuñas y guanacos. Ph. D. thesis, Fac. Agr. C. Vet., Buenos Aires 1927.

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A 'missing link' in the evolution of the egg pedicel in lacewings?

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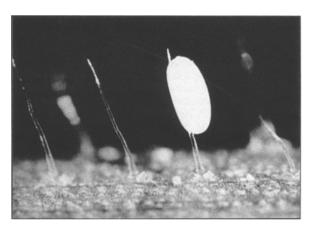
Swiss Federal Institute of Forestry Research, Division of Landscape Ecology, CH-8903 Birmensdorf (Switzerland), 7 August 1985

Summary. Brown lacewing eggs (Planipennia: Hemerobiidae) glued to the top of hairs of maize leaves can be seen as an intermediary evolutionary step between depositing the egg directly on the substrate (as in most neuropteroid families) and the protective behavioral adaptation of depositing the egg on a long thin pedicel (as e.g. in the Chrysopidae). Key words. Egg pedicel; evolution; lacewings; Hemerobiidae.

In several families of the insect order Planipennia the females regularly deposit their eggs on thin hyaline stalks. Egg pedicels have been described for some genera of the Mantispidae, Berothidae, Nymphidae and, most noticeable because of their worldwide distribution and abundance, the Chrysopidae.

In the common green lacewing, Chrysoperla carnea Stephens, the eggs are mostly deposited on the bottom side of leaves and twigs. While the egg is about 1 mm long, the length of the pedicel, depending on the size of the female, ranges from 3.5 to 6 mm². The selective advantage of a pedicel seems obvious, but few conclusive experiments have been published on that issue. The egg pedicel protects the egg from predation3, parasitization and cannibalism⁴. In the larger part of neuropteroid families, however, the eggs are glued to the substrate without a pedicel. The scattered occurrence of egg stalks in rather distantly related families in the order Planipennia⁵ suggests a polyphyletic origin

To be of selective advantage an egg stalk must be of a certain minimum length to effectively prevent predation and parasitism. It seems barely plausible to think of gradual evolutionary steps leading from an unprotected nonstalked to a well protected stalked egg, unless even a minute stalk provides a selective advantage under specific circumstances.



Egg of Micromus variegatus glued to a hair on the upper surface of a maize leaf.

While regularly monitoring aphidophagous insects in maize fields in northwestern Switzerland, a peculiar type of lacewing eggs on tiny stalks of 0.5-1 mm length was observed in small numbers. Closer examination revealed that they were in fact hemerobiid (brown lacewing) eggs deposited on plant hairs on the upper side of maize leaves (fig.). The Hemerobiidae normally do not produce egg pedicels, but here obviously take advantage of the hirsute surface of the plant leaf. Out of a total of 22 hemerobiid eggs collected on maize in summer 1983, 14 were attached close to the tip of hairs.

Subsequent inspection of 100 egg stalks of Chrysoperla carnea on maize leaves showed that they also were predominantly (91%) placed on top of hairs. The bottom sides of maize leaves bear no hairs, which might explain the observation that on this crop, contrary to the general habit, only about 10% of the eggs of C. carnea were found on the bottom side of the leaves.

The Hemerobiidae thus may represent an intermediate evolutionary step on the way to producing an egg pedicel. The behavioral adaptations of gluing an egg to the tip of a hair may have triggered the development of behavioral traits to first prolong that hair with the hyaline mucus which is used to glue the eggs to the substrate, and later to build a pedicel even without the aid of a supporting hair. This interpretation would go along with the observation that several chrysopid species with adults of rather small size show a tendency to deposit their stalked eggs on spines of leaves or tips of conifer needles (e.g. Cunctochrysa in Europa, Eremochrysa and Chrysopiella in the USA)4. Even Chrysoperla carnea, known to deposit its eggs on a large variety of substrates which often bear no hairs, will go back to the 'ancient' behavior as soon as hairs are available.

- Szentkirályi, F., (Plant Protection Institute, Budapest) found eggs of several hemerobiid species on hairs of maize leaves in Hungary (personal communication).
- Duelli, P., in: Biology of Chrysopidae, p. 129. Dr W. Junk Publ., The Hague 1984.
- Chen, S. H., and Young, B., Sinensia, Shanghai 12 (1941) 211. Duelli, P., and Johnson, J. B., unpublished results.
- Schlüter, T., in: Biology of Chrysopidae, p. 1. Dr W. Junk Publ., The Hague 1984.

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