

Le fractionnement de l'ARN global des souches sauvages étudiées a d'autre part révélé l'existence de différences très significatives quant à l'importance de certaines populations ribonucléiques de faible poids moléculaire. Les souches compatibles semblent être caractérisées par des pics de 5S et 4S assez élevés et vice versa. On note cependant que les souches compatibles S2 et S110 sont toutes deux de signe A, alors que S86' et S93', choisies pour leur croissance vigoureuse, sont du signe opposé a. Comparées à la souche S2 de même signe (a), il nous faut toutefois conclure que les présentes déviations diffèrent statistiquement de celles observées entre A et a lors de l'analyse d'un asque complet résultant du croisement S2A × S2a⁵.

Les expériences effectuées au cours de ce travail ne nous permettent pas d'attribuer définitivement ces variations à une diminution du taux de synthèse ou à une augmentation du taux de dégradation de l'ARN des souches incompatibles¹⁵; de même que nous ne pouvons établir avec certitude si cette disparition de certaines espèces d'ARN (qui nous semble plus que fortuite) joue un rôle fonctionnel significatif dans l'établissement de l'incompatibilité chez cet ascomycète. Il n'en demeure pas moins que la poursuite de ces travaux permettra peut-être de jeter un peu de lumière sur ce phénomène des plus intéressants mais combien négligé qu'est l'origine biochimique de la différenciation sexuelle chez les champignons.

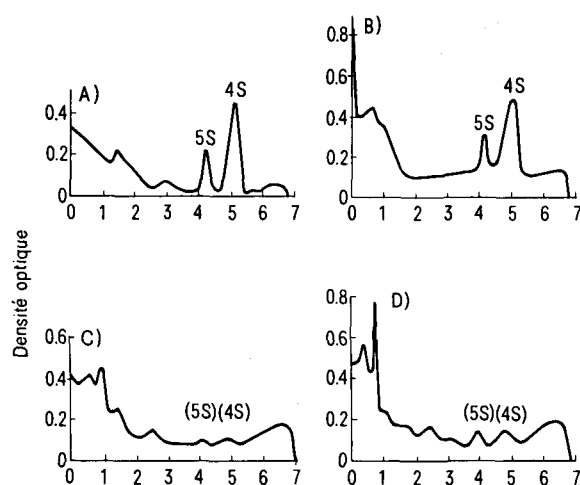


Fig. 2. Electrophorèse en gel de polyacrylamide 7.5% de l'ARN global des souches sauvages S2 (A), S110 (B), S86' (C) et S93' (D) d'*Ascobolus immersus*. Abscisse: distance parcourue en cm; ordonnée: densité optique à 260 nm.

Quantités relatives des différentes fractions en ARN telles que déterminées chez différentes souches sauvages d'*Ascobolus immersus* en comparant la hauteur des pics du profil électrophorétique selon la méthode décrite plus tôt^{5, 6, 15}

Souche	Signe	Rapports (%)		
		19S/25S	5-4S/25S	5S/4S
S2	A	92.9 ± 3.8	25.8 ± 1.0	37.3 ± 7.2
S2	a	93.0 ± 3.5	13.8 ± 3.1	56.3 ± 6.7
S110	A	91.1 ± 4.9	51.6 ± 3.0	49.1 ± 7.1
S86'	a	96.8 ± 1.6	6.9 ± 1.5	67.8 ± 12.8
S93'	a	91.8 ± 4.7	10.4 ± 2.9	109.7 ± 11.2

L'égalité des moyennes et des variances a été testée aux seuils de 5% et 1% en utilisant les distributions *t* et *F*, respectivement. Les valeurs obtenues pour la souche S2 de signe a⁵ sont également inscrites pour fin de comparaison.

Summary. Fractionation of total RNA prepared from intersterile wild type strains of *Ascobolus immersus* revealed the existence of differences at the 4S and 5S levels which may be related to the polymorphism of these species or sub-species, bearing the same name and coexisting along in nature.

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⁸ I. W. FULTON, Proc. natn. Acad. Sci., USA 36, 306 (1950).

⁹ C. A. RAPER et J. R. RAPER, Genetics 54, 1151 (1966).

¹⁰ J. R. RAPER, Genetics of Sexuality in Higher Fungi (Ronald Press, New York 1966).

¹¹ J. R. RAPER, G. S. KRONIGELB et M. G. BAXTER, Am. Nat. 92, 221 (1958).

¹² K. M. SWIEZYNSKI et P. R. DAY, Genet. Res. Cambridge 1, 114 (1960).

¹³ K. M. SWIEZYNSKI et P. R. DAY, Genet. Res. Cambridge 1, 129 (1960).

¹⁴ H. L. K. WHITEHOUSE, New Phytol. 48, 212 (1949).

¹⁵ C. HAMELIN et G. H. COUSINEAU, Rev. Can. Biol. 33, 247 (1974).

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Morphological Duality of the Retinal Pattern in Flies

In 1909, DIETRICH¹ described fundamental architectural plans of the fly-retina. Each ommatidium contains altogether 8 retinular cells, which, in transversal sections through the ommatidia, are arranged in an asymmetrical trapezium, the cells 1-3 lying always anterior. Cell 8 whose rhabdomere is situated in the centre of the intra-ommatidial cavity arises in the proximal part between the cells 1 and 2 (this arrangement is abbreviated here [1/8/2]). Retinular cell patterns of the dorsal and ventral retinal parts are arranged in a mirror-symmetry.

Although this plan [1/8/2] is a valid pattern for many species¹⁻⁵, in at least two families (Rhagionidae, Asilidae), another type, with cell 8 lying between cells 5 and 6

¹ W. DIETRICH, Z. wiss. Zool. 92, 465 (1909).

² O. TRUJILLO-CENÓZ, Cold Spring Harb. Symp. quant. Biol. 30, 371 (1965).

³ V. BRAITENBERG, Exp. Brain Res. 3, 271 (1967).

⁴ D. COSENS and M. M. PERRY, J. Insect Physiol. 18, 1773 (1972).

⁵ S. WADA, Z. Morph. Tiere 77, 87 (1974).

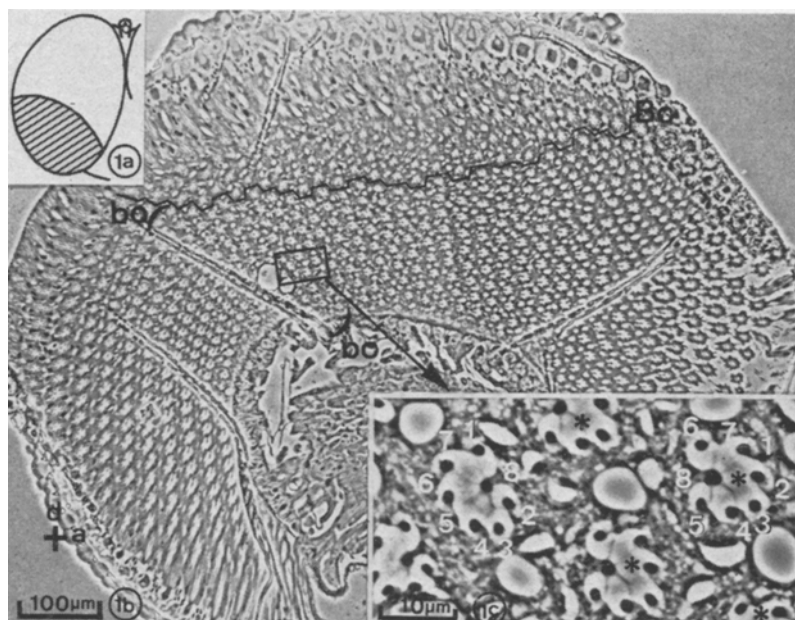


Fig. 1. *Rhagio scolopacea* ♂. Ventral retinal part showing the populations of ommatidia [5/8/6] (anterior; in c, with*) and [1/8/2] (posterior); a) locality of the section (hatched). The broken line (Bo) and (□)-zone (bo) show the borderline between the dorsal and ventral retinal parts and transitional zone between both population fields respectively. 1-8, reticular cells, numbering after DIETRICH¹; a, anterior; d, dorsal. Phase contrast.

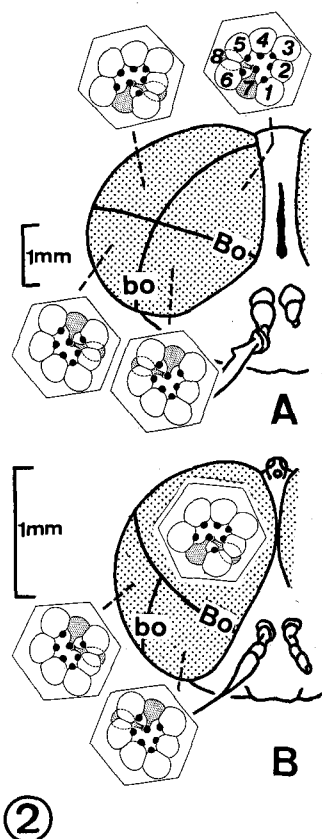


Fig. 2. Examples of the retinal pattern types A and B, with schemes of reticular cell arrangements, in front views of the heads of *Tabanus apricus* ♀ (A) and *Rhagio scolopacea* ♂ (B). Bo, bo see Figure 1 (the border topography was determined in histological preparations by the additional marking of different retinal areas with vulcanized animal hairs¹⁰; in A and B, without reference to the special ommatidia in antero-dorsal marginal zones of the compound eyes^{5,11}).

([5/8/6]), was also observed⁵. These ommatidia were found to be situated beside the population of ommatidia [1/8/2]. TRUJILLO-CENÓZ and BERNARD⁶ reported that, in the females of two Dolichopodid species, cell 8 lies between cells 5 and 6.

The present study attempted firstly to establish whether the ommatidium [5/8/6] is also a regular pattern (e.g. not a 'situs inversus'); secondly, if it is of constant occurrence, to ascertain the topography of ommatidia [5/8/6] and [1/8/2] in the retina; and finally, to compare the retinal patterns of different species in the main systematic groups of flies.

48 species from 26 families were examined; compound eyes were fixed in Bouin's solution, embedded in a plastic mixture (methyl methacrylate – polyethylene glycol), cut at 1–2 μ m in serial sections, and observed by means of phase contrast⁵. In all 24 representatives of 9 families the dual retinal structure occurred constantly. The regular ommatidia [5/8/6], and ommatidia [1/8/2] are so patterned that, enclosed in their respective population fields, ommatidia [5/8/6] lie always in the anterior area, [1/8/2] in the posterior one. Only in the transitional zone, usually extending over a few ommatidial rows, are both types mixed (Figure 1). The topography of the border between both population fields varies as to species (and for certain species, e.g. in *Rhagio*, to sex, or to the dichoptic and holoptic condition).

The diverse patterns showing this morphological duality are classifiable into 2 types. A) In both dorsal and ventral retinal regions, ommatidia [5/8/6] fill the anterior parts, [1/8/2] the posterior ones (Figure 2, A). B) Only ommatidia [1/8/2] occur over the entire dorsal region, whereas ommatidia [5/8/6] are situated antero-ventrally and [1/8/2] postero-ventrally (Figure 2, B). Within this pattern, however, single ommatidia [5/8/6], strewn in a few ommatidial rows of the antero-dorsal marginal area, have sometimes been observed. The retina consisting only of ommatidia [1/8/2], as shown by DIETRICH¹, is described here as type C.

The species used here, and their retinal pattern types, were arranged into a model⁷ of the evolutionary tree (Figure 3). Type A has been found predominantly in Brachycera Orthorrhapha. In both Lonchopteridae and

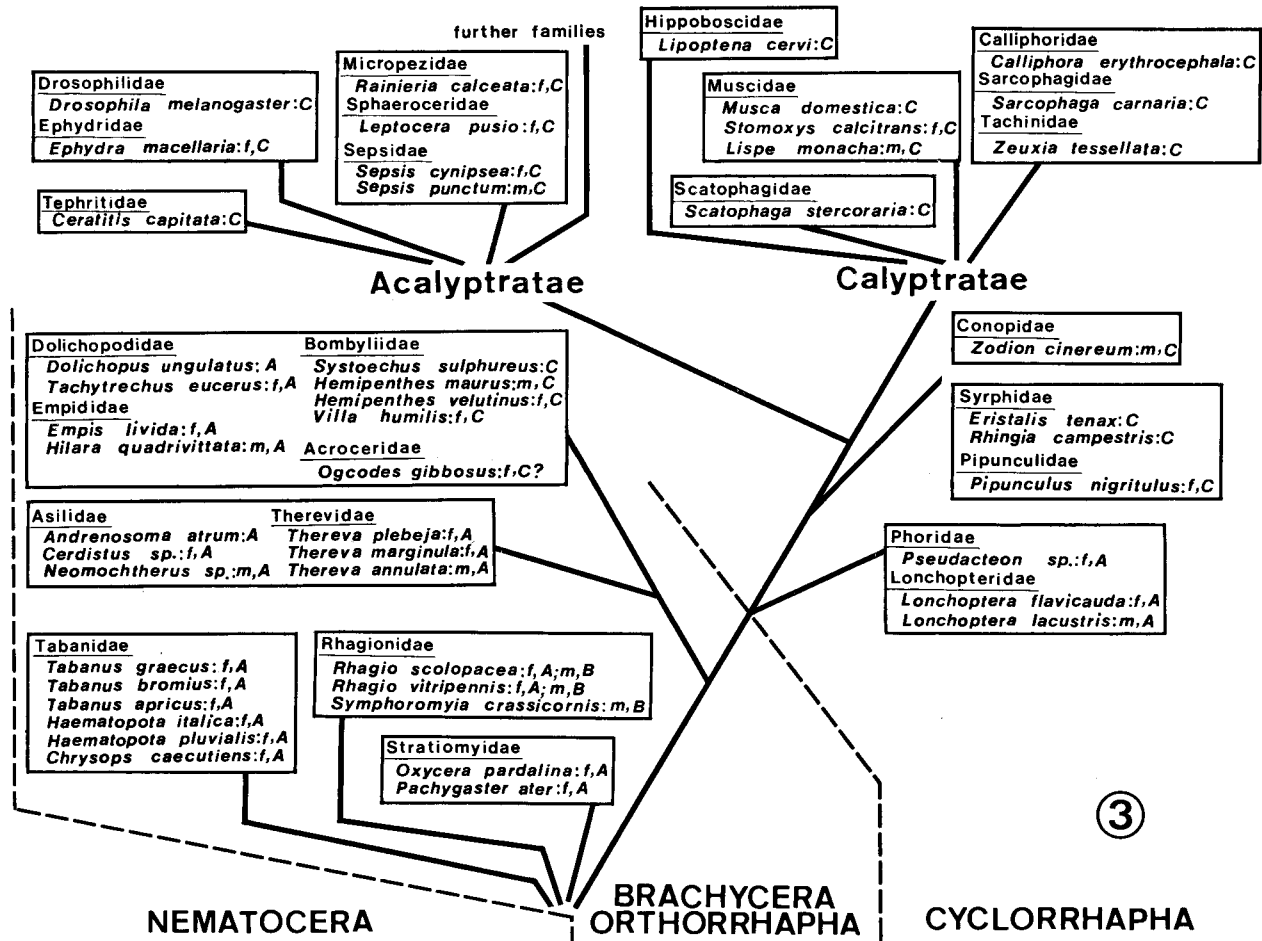


Fig. 3. The species examined and their retinal pattern types are arranged into a dendrogram after the OLDROYD-model⁷ showing the phylogenetic relationships of the main groups of flies¹². A, B and C after the species' names indicate their individual retinal types (see text). f, ♀; m, ♂; results without f and m are valid for both sexes (*Pipunculus nigritulus* = *Toemoesvaryella geniculata*).

Phoridae, primitive families very probably belonging to the Cyclorrhapha^{7,8}, the retina also revealed type A. Type B has been observed until now only in ♂♂ of Rhagionidae. Type C is distributed in almost all sections of Cyclorrhapha; also in Bombyliidae. *Sympycnus lineatus*⁶ was not examined here, hence it is still uncertain whether its retina, like its Dolichopodid sister-groups studied here, is of type A.

Although the reconstruction of the close relationship of the Bombyliidae to the Asiloidea, as shown in the model, has not yet been definitely established^{8,9} the facts described above may indicate that the dual retinal structure is to be found in the primitive flies, whereas the 'uniform' retina, containing only ommatidia [1/8/2], is present in the families of more advanced evolution. Since flies proper, in contrast to the Nematocera, can be undoubtedly regarded as a monophyletic unit⁸, these retinal patterns might have undergone evolutionary transformation from one type to another in the phylogeny of flies. Further investigations are in progress.

Summary. In the compound eyes of flies, a morphological duality of the retinal structure has been found. The retinal patterns based on this property and their possible evolutionary trends are described.

Zusammenfassung. In den Komplexaugen der Fliegen wurde eine morphologische Dualität der retinalen Struk-

tur gefunden: Die Retina besteht aus Ommatidien zweier Typen, die jeweils einen geschlossenen Populationskreis bilden. Die Morphologie der hierdurch hervorgerufenen retinalen Muster und die mögliche evolutionäre Tendenz ihrer Verbreitung in den Brachycera-Orthorrhapha und den Cyclorrhapha wurden beschrieben.

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⁶ O. TRUJILLO-CENÓZ and G. D. BERNARD, J. Ultrastruct. Res. 38, 149 (1972).

⁷ H. OLDROYD, *The Natural History of Flies* (Norton, New York 1966).

⁸ W. HENNIG, *Handbuch der Zoologie* (W. De Gruyter, Berlin 1973), vol. 4, part 2.

⁹ M. MÜHLENBERG, Z. Morph. Tiere 70, 73 (1971).

¹⁰ S. WADA, Int. J. Insect Morph. Embryol. 3, 397 (1974).

¹¹ S. WADA, Experientia 27, 1237 (1971).

¹² Conopidae are another family that ... have followed a divergent line of evolution, leading them away from close relationships with any other living flies... We may take advantage of the fact that this is a work of natural history, and consider them alongside the hover-flies, rather than in their true systematic position (ref.⁷, p. 168).

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