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Systematics, ecology and biogeographical relationships in the sub-family Traviinae (Polychaeta, Opheliidae)

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ABSTRACT

The Opheliidae is divided into three monophyletic groups corresponding to the three sub-families defined by HARTMANN-SCHRÖDER: Ophelininae, Opheliinae and Traviinae. The object of the current paper is to offer a contribution to the knowledge of the sub-family Traviinae including taxonomy, ecology, biogeographical distribution. Three genera are studied: *Dindymenides*, *Kesun* and *Travisia*. Based on previous phenetic and phylogenetic studies of the family and sub-families, we propose to consider *Travisia* as the only valid genus in the sub-family. Twenty-seven species and three sub-species are recognized in this genus. However, many of them are incompletely described and the characters used in species-recognition varies from one author to the next and the validity on some characters has not been recognized until recently. Most of the species must be redefined based on recent findings; we are, however, able to propose a preliminary key to species. Species of *Travisia* general inhabit a muddy substratum, from the intertidal to abyssal depths (7,800 m). Twenty-one taxa are found on the continental shelf and 14 of these are limited to shelf depths (< 200 m). Eleven taxa are found at depths below 2,500 m; three are strictly abyssal. The genus shows a world-wide distribution, but is especially well represented in the Pacific Ocean (21 taxa). Seven taxa are found in the Antarctic Ocean and 10 in the Atlantic Ocean. Sixteen taxa are exclusively to the Pacific Ocean. Eight species with a large geographical range also show extended bathymetric ranges: *T. glandulosa*, *T. forbesi*, *T. fusus*, *T. gravieri*, *T. japonica*, *T. kerguelensis*, *T. olens*, and *T. profundus*. A study of the relationship between species and biogeographical distribution is given.

RÉSUMÉ

Systématique, écologie et relations biogéographiques dans la sous-famille des Traviinae (Polychètes, Opheliidae)

L'ensemble des données sur la famille des Opheliidae a été réuni afin de fournir un état actuel des connaissances sur cette famille. Les Opheliidae se divisent en trois groupes monophylétiques correspondant aux trois sous-famille décrites par HARTMANN-SCHRÖDER : Ophelininae, Opheliinae et Traviinae. L'objectif de cette note est de fournir une revue des connaissances sur la taxonomie, l'écologie, la distribution biogéographique de la sous-famille des Traviinae. A partir de considérations phénétiques et phylogénétiques, il est proposé de réunir les trois genres décrits : *Dindymenides*, *Kesun* et *Travisia*, dans le seul genre *Travisia*. Vingt-sept espèces et trois sous-espèces peuvent être reconnues comme valides, cependant beaucoup d'espèces demeurent incomplètement décrites et les caractères morphologiques utilisés changent d'un

auteur à l'autre. Bien que la plupart des espèces mérite de nouvelles observations, il est proposé une clé préliminaire d'identification des espèces du genre *Travisia*. Le genre est typique des substrats vaseux, il est rencontré depuis la zone intertidale jusqu'aux abysses (7800 m). Vingt-et-un taxons sont connus du plateau continental, 14 ne dépassant pas ce plateau. Onze taxons ont été recensés à des profondeurs inférieures à 2500 m, trois d'entre eux sont strictement abyssaux. Le genre a une distribution cosmopolite, mais il est particulièrement bien représenté dans l'océan Pacifique (21 taxons). Sept taxons sont antarctiques, 11 atlantiques, 16 sont exclusifs du Pacifique. Huit espèces ont une large distribution géographique et bathymétrique : *T. glandulosa*, *T. forbesi*, *T. fusus*, *T. gravieri*, *T. japonica*, *T. kerguelensis*, *T. olens*, et *T. profundus*. Les relations biogéographiques entre les espèces ont été recherchées.

INTRODUCTION

During the course of our research, we have had the opportunity to study the species belonging to family Opheliidae, including the genus *Ophelia* (BELLAN & DAUVIN, 1991; BELLAN-SANTINI *et al.*, 1992), and the family in general (BELLAN *et al.*, 1990). In this last paper, the 12 genera of the family were analyzed to attempt a coherent classification of the family. Our results confirm the subdivision into three sub-families originally proposed by HARTMANN-SCHRÖDER (1971): Ophelininae, Opheliinae and Traviinae. This last sub-family seems particularly suitable to be studied because of the small number of accepted genera: *Dindymenides*, *Kesun* and *Travisia*, its plesiomorphy, and its undespread ecological and geographical distributions. Nevertheless, one of the difficulties lies in the incomplete description of many species, and the non-existence of type specimens. The lack of accuracy of descriptions is due, usually, to age of the specimens, and the small number of specimens described, but it is also necessary to point out the difficulties inherent to the morphological criteria used for these descriptions. Our major objectives are to present the various problems remaining within the sub-family Traviinae, to present the state of the knowledge on this sub-family with a preliminary key, to discuss the generally admitted viewpoints, and to propose a certain number of interpretations and hypothesis as a basis for future work.

TAXONOMIC STATUS OF GENERA AND SPECIES OF TRAVIINAE

The sub-family Traviinae may be defined as following:

Opheliidae with short and grublike body, without lateral and ventral grooves or with very reduced grooves. Branchiae generally present, posterior setigers generally with epipodial pads. Anal cylinder usually short, sometimes furrowed, anal cirri short, and thick setae smooth or finely spinose.

The genus *Travisia* was first described by JOHNSTON (1840) as:

Diagnosis: Body short, fusiform or grublike, without distinct groove. Prostomium small, cone-shaped, two nuchal organs. Branchiae present, lateral eyes absent; posterior epipodial pads more or less developed. Parapodial small, without presetal lobes. Lateral sense organs present between parapodial rami. Anal cirri usually short and thick. Setae simple, capillary, or hispid. First setiger appears before the mouth.

Two other genera have been described: *Dindymene* Kinberg, 1866, and *Kesun* Chamberlin 1919.

Diagnosis: *Dindymene* Kinberg, 1866 "Corpus fusiforme, segmenta 3-2 annulata, lobus cephalicus minutus, terminalis, nudus; segmenta buccalia tria, primum nudum; os inferum, transversum; pharynx sine papillis et maxillis; pedes duplices, distantes, setis capillaribus: aliis laevibus, aliis serrulato-ciliatis; branchiae cirrosae, usque a segmento buccali secundo; segmenta posteriora tuberculis binis utrinque praedita".

CHAMBERLIN (1919) renamed this genus *Dindymenides* since the original name has been used in 1847 for a Crustacean. He does not give more details on the diagnosis of the genus.

BELLAN *et al.* (1990), following FAUCHALD (1977), kept *Dindymenides* as a valid genus on the basis of a strong autoapomorphy: the serrulate-ciliate setae. However, these authors pointed out that these characters needed to be confirmed. A certain number of Traviinae belonging to genus *Kesun* and *Travisia* have been also described with hispid and/or serrulated setae. HARTMAN (1948), who examined the Kinberg's material, did not mention these ornamentations. If we consider the position of the first setae with regard to the mouth, HARTMAN stated that the prostomium of the preserved specimen had been unnaturally flattened in a vial, resulting in the misinterpretation of the anterior part of the animal. HARTMAN stated: "the first setae are in front of the oral aperture". Considering the wide variations of the body of the Traviinae due to their conservation, we accept the opinion of HARTMAN at least until we are in position to examine freshly material. *Dindymene* and thus also *Dindymenides* is known only from a single record (DAY, 1967). In summary, we prefer to consider this genus

invalid, following the opinion of HARTMAN (1948), and more recently FAUCHALD (*in litt.*). The only species known in the genus, originally described as *Dindymene concinna*, must now be known as *Travisia concinna* (KINBERG, 1866).

Diagnosis: *Kesun* Chamberlin, 1919. "Body short, pointed at both ends, fusiform or grub-like. Body rounded cylindrically, without ventral groove. Somites of the middle region triannulate, the others may be only biannulate or entire. Prostomium small, wholly smooth and rounded, without processes. Parapodial tubercles small and smooth, or wholly absent. No cirri or branchia on any somite. No eyes. With a series of lateral sensory pits as in *Travisia*. Pygidium small, cylindrical, longitudinally furrowed. Segments not numerous (twenty-eight in the type)".

Kesun was created by CHAMBERLIN (1919) for a species *Kesun fusus* distinguishable from the other species of *Travisia* described at that time, by the lack of "cirri" which are commonly interpreted as branchiae. Another feature is the absence of epipodial pads on the last segments and the presence of an anal cylinder. Accepting for the moment the absence of branchiae as a characteristic feature of the genus *Kesun*, we have to point out that other features mentioned, such as the anal cylinder and the lack of epipodial pads in the last setigers are not unique to abrianchiate members of the sub-family. The anal cylinder of *K. fusus* is very short and not really distinguishable from that of *Travisia profundus* and from many other species of the genus. The absence of epipodial pads is also not a unique feature either. This leaves only one unequivocal difference between *Travisia* and *Kesun*: the absence of branchiae in the latter. In a previous paper, BELLAN *et al.* (1990) argued that this character should not be used at a generic level. The fact that members of *Kesun* are limited to bathyo-abyssal depths might be used as a characteristic feature; however this present time, we propose to discard *Kesun* and retain only a single genus, *Travisia*. HARTMAN (1965a) had already proposed this synonymy. The definition of the genus corresponding to that of the sub-family Traviinae with a supplementary character: the presence of pustulae or similar structure on the body.

The fact that remains only one genus *Travisia* in the Traviinae should not change the status of this sub-family. In BELLAN *et al.* (1990), the classification of the Opheliidae family was made using sequencing which means that the first taxa (Traviinae) is the sister group of all following groups with a rooted tree by a theoric ancestor (see WILLEY, 1981). This classification taking into account the level of apparition in the cladogram was:

- Family Opheliidae
 - Sub-family Traviinae
 - Sub-family Opheliinae
 - Sub-family Ophelininae

This classification regards the very strong differentiation between the Traviinae and the group Opheliinae + Ophelininae, and respect the classical use of the three sub-families. In the present state of the knowledge, it is not possible to state on the filiation between the Opheliinae and Ophelininae.

ANALYSES OF TRAVISIINAE SPECIES

We have observed available types or specimens from 21 taxa. The examined specimens come from: 1) Natural History Museum, London, 2) Smithsonian Institution, Washington, 3) Muséum National d'Histoire Naturelle and 4) National History Museum of Los Angeles County. The numbers at the end of these 21 species refer to the museum where they are deposited. A lack of a number indicates that we did not see the specimen. Twenty-seven species and three sub-species are now retained. The alphabetical list of these taxa with indication of the most complete description available, the list of authors having cited the species, and their known geographical distribution is given below:

- *T. antarctica* Hartman, 1967, pp. 139-140; HARTMAN, 1978. South Georgia, Antarctic, South Atlantic Ocean; 2,452-2,727 m. (2)
- *T. arborifera* Fauvel, 1932, pp. 191-193, fig. 33; FAUVEL, 1953. Andaman sea, Gulf of Bengal; British Natural History Museum Collection, 1 ex. off Burma coast, 35 m. Indian Ocean. 7-100 m. (1)
- *T. brevis* Moore, 1923, pp. 220-221; BERKELEY & BERKELEY, 1952, pp. 90-91, fig. 183; BANSE & HOBSON, 1968; HARTMAN, 1969, pp. 343-344, 1 fig. BERKELEY & BERKELEY, 1942; IMAJIMA, 1961, 1963, 1964; REISH, 1965; HARTMAN, 1961, 1965b, 1969; FAUCHALD, 1972; LOI, 1980; HOBSON, & BANSE, 1981; FAUCHALD & HANCOCK, 1981. Southern California, North-eastern Pacific, Bering Sea, Okhotsk Sea. 18-2,900 m. (2)
- *T. carnea* Verrill, 1873, pp. 508 & 604; EHLERS, 1887; PETTIBONE, 1954, pp. 296-298; APPY *et al.*, 1980. According to HOBSON & BANSE, 1981, the designation of *T. carnea* by BERKELEY, 1966, 1968 for British

- Columbia is incorrect; it is probably *T. pupa*. We have seen the holotype of *T. parva* Day, 1973 (p. 94, fig. 13), off Beaufort, North Carolina. It has: 20 setigers, a posterior asetigerous segment, 19 pairs of branchiae, neither parapodial lappets nor lateral crenulations. These characters are very similar of those of *T. carnea* Verrill, 1873, and it is surprising that DAY didn't compare his species with the Verrill's species which are found in the same area and depth. We consider *T. parva* as a synonym of *T. carnea*. North-western Atlantic, Massachusetts to Long Island, Arctic Alaska. 5-35 m. (2)
- *T. chilensis* Kükenthal, 1887, pp. 364-365, figs 1-3. Chiloe, South-eastern Pacific.
 - *T. chinensis* Grube, 1869, p. 66; AUGENER, 1922, pp. 38-40. China Sea, North-western Pacific.
 - *T. concinna* (Kinberg, 1866), p. 256; KINBERG, 1910, p. 66, plate 25, fig. 5; HARTMAN, 1948, pp. 113-114. Algoa Bay, South Africa, 5-20 m.
 - *T. doellojuradoi* Rioja, 1944, pp. 135-136, figs 57-59; RIOJA, 1946. Argentina coasts, South-western Atlantic. 115 m.
 - *T. elongata* Grube, 1866, p. 66; EHLERS, 1901, p. 171, plate 22, figs 11-14. AUGENER, 1922, p. 34. Iquique, Peru, South-eastern Pacific.
 - *T. foetida* Hartman, 1969, pp. 344-345, three figures; FAUCHALD, 1972, pp. 237-238, plate 49, fig. d; FAUCHALD & HANCOCK, 1981; MOORE, 1923, HARTMAN, 1963, 1965b, 1966a as *T. pupa*. Redondo Canyon, California, North-eastern Pacific. 250-3,100 m. (4)
 - *T. forbesii* Johnston, 1840, pp. 373-374, plate 19, figs 11-18; RATHKE, 1843, pp. 192-194, plate 10, figs 9-12. de SAINT JOSEPH, 1898; McINTOSH, 1908a, b; FAUVEL, 1914, 1925; ANNEKOVA, 1937, 1938; BERKELEY & BERKELEY, 1942; STÖP-BOWITZ, 1945, 1948; WESENBERG-LUND, 1950, 1951; PETTIBONE, 1956; CHLEBOVITSCH, 1961; DAY, 1961, 1967; ELIASON, 1962; HARTMAN, 1965a; HAMOND, 1966; CABIOCH *et al.*, 1968; RETIÈRE, 1968; GLÉMAREC, 1969; KIRKEGAARD, 1969; AMOUREUX, 1971; LEVENSTEIN, 1966, 1971/72; WOLFF, 1973; AVERINCEV, 1977; HOLTHE, 1977; HOBSON, & BANSE, 1981. According to STÖP-BOWITZ (1948) and as EHLERS (1897), the designation of *T. forbesii* from the coasts of Chile and Antarctic is doubtful. *T. forbesii* is characteristic of the northern hemisphere where it is collected to 300 m (LEVENSTEIN, 1971/72). One specimen of *T. forbesi* with 28 setigers from False Bay, South Africa, is in the collection of the Natural History Museum of London. We confirm the presence of the species in South Africa. Arctic, Circumpolar: Novaya Zemlya, Davis Strait, Spitsbergen, Kara sea, Alaska and Canadian Arctic, North-east America, Siberia, Bering sea to Washington Sound, North Japan Sea, West and east Greenland, Iceland, Faroes, Norway, North sea, western Baltic, Great Britain, France; off the mouth of the Amazon, Brazil, South Africa. 0-3,000 m. (1, 3)
 - *T. forbesii intermedia* (Annenkova, 1937), p. 177; USCHAKOV, 1955; BUZHINSKAYA, 1985. According to BUZHINSKAYA (1985), we have considered *T. kerguelensis* McIntosh subsp. *intermedia* Annenkova, 1937 as a *T. forbesi* subsp. *intermedia* (Annenkova, 1937). Japon Sea, North-western Pacific. 30 m to abyssal.
 - *T. fusiformis* Kudenov, 1975, pp. 215-218, figs 17-23. Gulf of California, Mexico, North-eastern Pacific. Intertidal. (4)
 - *T. fusus* (Chamberlin, 1919), p. 386, plate 67, fig. 5 and plate 68, figs 1-2; LEVENSTEIN, 1970, 1971/72. Pacific Ocean. 3,000-7,580 m. (2)
 - *T. gigas* Hartman, 1938, p. 103, figs 46-48; HARTMAN, 1961, 1963; BERKELEY & BERKELEY, 1941, 1962; BERKELEY, 1968; REISH, 1968; HOBSON & BANSE, 1981. California, North-eastern Pacific. 0-180 m. (2)
 - *T. glandulosa* McIntosh, 1879, p. 506, figs. 15-16. We have seen the only known specimen of *T. glandulosa*. It was found in North-western Atlantic at 3,300 m. It has: 7 mm length, no visible branchiae, a very distinct lateral groove at the last setigers, pustulae in a row by annulus. These characters are very similar to those of *Kesun abyssorum* Monro, 1930. Even if *T. glandulosa* was rather poorly described by McINTOSH, it does not seem that Monro compare his specimen with McINTOSH's species. Considering the similarity of *Kesun abyssorum* Monro, 1930 with *Travisia glandulosa* McIntosh, 1879, we propose the synonymy of the two species. MONRO, 1930, p. 167, fig. 69 8 8; KIRKEGAARD, 1956, p. 71, fig. 10; HARTMAN, 1966b, p. 51; MONRO, 1939; AUGENER, 1932; HARTMAN, 1967; LEVENSTEIN, 1961a, 1961c, 1971/72, 1975, 1978; AVERINCEV, 1974; ROZBACZYLO, 1985. Pacific Ocean, Antarctic Ocean, Atlantic Ocean. 193-6,850 m. (1)
 - *T. granulata* Moore, 1923, pp. 219-220; HARTMAN, 1938, 1961, 1969; LOI, 1980. Southern California, North-eastern Pacific. 45-105 m. (2)
 - *T. gravieri* (McINTOSH, 1908a), pp. 383-384; McINTOSH, 1915, pp. 29-30, plate 95, fig. 8; HARTMAN, 1965a, pp. 191-192; HARTMAN & FAUCHALD, 1971; LEVENSTEIN, 1971/72; AMOUREUX, 1982; KIRKEGAARD, 1980. Atlantic Ocean. 539-7,800 m. (1)
 - *T. hobsonae* Santos, 1977, pp. 559-564, fig. 1; UEBELACKER, 1984, pp. 17-4, 17-5, figs 17-1, 17-2. Gulf of Mexico, North-western Atlantic. 10-110 m. (2)

- *T. horsti* Caullery, 1944, pp. 47-48, fig. 40. Java Sea, Pacific. 959 m.
- *T. japonica* Fujiwara, 1933, pp. 91-103, plate I, figs 1-8, plate II, figs. 1-6; MONRO, 1934, pp. 373-374, fig. 8 as *T. chinensis* Grube, 1869 according to HARTMAN, 1959; FAUVEL, 1936, pp. 75-78. FAUVEL, 1933; USCHAKOV, 1955; IMAJIMA & HARTMAN, 1964, BERKELEY, 1966; UCHIDA, 1967; HOBSON & BANSE, 1981; FOURNIER & LEVINGS, 1982; BUZHINSKAYA, 1985. Japan Sea, North-western Pacific. 10-105 m. (1, 3)
- *T. kerguelensis* McIntosh, 1885, pp. 357-359, plate 43, fig. 10, plate 36A, figs 1-2; EHLERS, 1897, pp. 97-98, plate 6, figs. 159-161; AUGENER, 1922, pp. 36-37; HARTMAN, 1966b, p. 54, plate 17, figs 4-5; AVERINCEV, 1982, p. 34, plate 5, figs 12-14; EHLERS, 1901, 1908, 1912; AUGENER, 1923, 1932; MONRO, 1930, 1936, 1939; FAUVEL, 1941; RIOJA, 1944, 1946; HARTMAN 1953, 1967, 1978; KNOX, 1962; AVERINCEV, 1974; DAY & HUTCHINGS, 1979; ROZBACZYLO, 1985; HARTMANN-SCHRÖDER, 1986; HARTMANN-SCHRÖDER & ROSENFELDT, 1989. Kerguelen, Southern Indian, Southern Atlantic, Antarctic Ocean. 0-1,837 m. (1, 3)
- *T. kerguelensis gravieri* Monro, 1930, p. 167, fig. 68; HARTMAN, 1966b; HARTMANN-SCHRÖDER & ROSENFELDT, 1989. Palmer Archipelago, Antarctic Ocean. 259-315 m. (1)
- *T. lithophila* Kinberg, 1866, p. 256; AUGENER, 1922, pp. 32-33; HARTMAN, 1966b, p. 54, plate 17, figs 7-10. HUTCHINGS & MURRAY, 1984, p. 79; HARTMAN, 1952. Australia, South-western Pacific. 20-180 m.
- *T. nigrocincta* (Ehlers, 1913), p. 525; HARTMAN, 1966b, 1967. South Pacific, Antarctic. 2,725 m.
- *T. olens* Ehlers, 1897, p. 98-99, plate 6, figs 162-163; AUGENER, 1922, pp. 35-36; EHLERS, 1901, 1912; MONRO, 1930; AUGENER, 1932; BENHAM, 1950; HARTMAN, 1966b, 1967; DAY & HUTCHINGS, 1979. HARTMANN-SCHRÖDER & HARTMANN, 1980; ROZBACZYLO, 1985. One ex. Discovery st 939, 08/18/1932, 35°49'6S-173°27'E, 87 m. The designation of *T. olens* by FAUVEL, 1943 from California was probably incorrect, HARTMAN, 1969 did not cite the species from California. It may be *T. granulata*. Cape Horn, Scotia Sea, South-western Atlantic, Antarctic, New Zealand, South-eastern Pacific. 0-1,120 m. (1)
- *T. olens* Ehlers *novae zealandiae* Benham, 1927, pp. 123-128, plate 2, figs 70-72. EHLERS, 1897, 1907, 1912 as *T. olens*; BENHAM, 1950, DAY & HUTCHINGS, 1979. British Natural History Museum Collection: 9 ex. from Portobello. South Island, New Zealand. New Zealand, South-western Pacific. 0-20 m. (1)
- *T. oregonensis* Fauchald & Hancock, 1981, p. 19. Offshore Oregon, North-eastern Pacific. 1,600-1,800 m. (4)
- *T. profundus* Chamberlin, 1919, pp. 387-389, plate 67, figs 1-4; USCHAKOV, 1955; KIRKEGAARD, 1956; LEVENSTEIN, 1960, 1961a, b, 1966, 1970, 1971/72, 1975, 1978; HARTMAN, 1967. Atlantic (Angola) and Pacific Ocean (Mid Basin), Antarctic Ocean. 975-7,290 m. (2)
- *T. pupa* Moore, 1906, pp. 228-230, plate 11, fig. 29; TREADWELL, 1914; USCHAKOV, 1955; LEVENSTEIN, 1960, 1961b, 1966, 1971/72; HARTMAN, 1961; BERKELEY, 1966, 1968; BERKELEY & BERKELEY, 1942, 1952; HOBSON & BANSE, 1981. North eastern Pacific. 33-3,012 m. (2)

DISCUSSION OF THE MORPHOLOGICAL CHARACTERS

The shared characters of all species of *Travisia* include the presence of nuchal organs and interramal sense organs; the capillary setae are often hispid and all species lack eyes. Characters used to distinguish the species include the presence of lobes or papillae on the pygidium, the position of the nephridiophores and the total number of setigers present. Few characters are unique to a single taxon. The body-shape is more variable, more or less fusiform or grub-shaped, but the shape may vary with the numbers of segments present and with the quality of fixation. The prostomium is pointed in all species, except in *T. foetida*, which is truncate. Lateral and mid-ventral grooves are generally absent; the development of these grooves characterize the different sub-families, however they are present, but poorly developed in some taxa. For example, a short lateral groove is present in *T. glandulosa* and a mid-ventral one in *T. fusiformis*, *T. gravieri* and *T. hobsonae*. Branchiae are present except in the species being transferred from *Kesun*: *T. fusus*, *T. glandulosa*, *T. gravieri*, and *T. nigrocincta*. The branchiae are cirriform except in *T. arborifera* which has branching branchiae. They are present from setiger 2, except in *T. hobsonae*, sometimes in *T. carnea*, and *T. profundus* where they are present from setiger 3. Unusual lobes or papillae are present on the pygidium in *T. japonica*, *T. gigas*, *T. kerguelensis gravieri*. Nephridiopores are present on setigers 3-14 except in *T. brevis* (7-25), *T. chiloensis* (7-14?), *T. japonica* (11-14 in the original description but 3-14 in Fauvel, 1933). The number (n) of setigers is relatively stable in a given species ($n \pm 5$) except in *T. granulata* 32-50, *T. japonica* 32-39 and *T. lithophila* 44-53. It would be interesting to study the actual significance of this variability as a possible character at the specific level.

A last point, is the variability of the degree of papillation in the posterior segments as described in *T. kerguelensis* by MONRO (1930). Some difficulties remain in ascertaining the identity of four similar taxa, all

described from southern oceans. They were distinguished on the number of segments and the papillation: *T. kerguelensis* (23-27 segments), *T. kerguelensis gravieri* (25), *T. olens* (29-36), and *T. olens novae zealandiae* (38-40).

PRELIMINARY KEY TO THE TRAVISIINAE

A preliminary key of the species *Travisia* is presented which is provisional due to the difficulties in correctly interpreting the available descriptions, some of which are incomplete. The need of a phenetic and phylogenetic study is necessary in order to test the validity of characters. Before, this can be done, it is necessary to have a complete redescription for all species. The following characters must be accurately described in all species:

- color and shape of live specimen;
- presence, shape, and variability of posterior lateral crenulations and parapodial lappets;
- number and variability of number of segments and setigers;
- number of branchiae;
- distribution of pustulae on the body;
- shape of the pygidium and pygidial papillae.

1	Branchiae absent	2
	Branchiae present	5
2	Lateral groove in the last 10 segments..... <i>T. glandulosa</i>	
	Lateral groove absent	3
3	Body grub-shaped, < 25 segments, mid-ventral groove present, very short setae <i>T. gravieri</i>	
	Body fusiform, ≥ 25 segments, fascicles of distinguished setae	4
4	Segment number 28, ≥ 25 setigers	<i>T. fusus</i>
	Segment number 25, 17 setigers.....	<i>T. nigrocincta</i>
5	Prostomium truncated, 31 setigers, large species.....	<i>T. foetida</i>
	Prostomium pointed conical	6
6	Branchiae branched	<i>T. arborifera</i>
	Branchiae cirriform	7
7	Mid-ventral groove present	8
	Mid-ventral groove absent	9
8	Mid-ventral groove slightly developed, 30-31 setigers, parapodial lappets developed ..	<i>T. hobsonae</i>
	Mid-ventral groove and parapodial lappets well developed, 34-35 setigers.....	<i>T. fusiformis</i>
9	Segment number > 40.....	10
	Segment number ≤ 40.....	13
10	Posterior parapodia with lobes or lappets	11
	Posterior parapodia without lobes or lappets	12
11	Posterior parapodia with triangular lappets, pygidium collarlike with 6 long dorsal papillae, length about 10 cm.....	<i>T. gigas</i>
	Posterior parapodia with small lappets, knob pygidium, length about 3 cm	<i>T. elongata</i>
12	Epithelium with large, dorsal and ventral coarse pustules, setiger number to about 45, pygidium with 12-13 irregular papillae.....	<i>T. granulata</i>
	Epithelium finely reticulated, from 44 to 53 setigers, pygidium with 7 cirri	<i>T. lithophila</i>
13	Segment number > 30	14
	Segment number ≤ 30	18
14	Posterior lappets absent, 26-45 setigers	<i>T. granulata</i>

Posterior lappets and lateral crenulations developed.....	15
15 Pygidium with an oval ventral lobe and 6 laterodorsal palpi	16
Pygidium shape otherwise	17
16 Laterodorsal palpi well developed, segment number 32-39, 26-32 branchiae pairs	<i>T. japonica</i>
Segment number 35, 33 pairs of branchiae	<i>T. concinna</i>
17 Segment number 29-32	<i>T. olens</i>
Segment number 38-40	<i>T. olens novae</i>
<i>zealandia</i>	
18 Setigers number = 18, 23 segments	<i>T. orogenensis</i>
Setigers number ≥ 20	19
19 Parapodial lappets reduced or absent	20
Parapodial lappets present	23
20 Setigers number ≥ 20 , 25-29 segments, pygidium small, longitudinally furrowed	<i>T. carnea</i>
Setigers number ≥ 25	21
21 Numbers of branchiae pairs 9-12, 26 setigers and 25-27 segments	<i>T. profundus</i>
Numbers of branchiae ≥ 15	22
22 Segments number 30-32, 25-28 setigers, 22-25 pairs of branchiae number	<i>T. pupa</i>
Segments number < 30 , about 25 setigers, 17-21 pairs of branchiae, anal cylinder surrounded by a circlet of short papillae	<i>T. antarctica</i>
23 Body pigmented in red purple, 17 pairs of branchiae	<i>T. doellojuradoi</i>
Body not pigmented in red purple, ≥ 18 pairs of branchiae	24
24 2 posterior achaetous segments	25
3-5 posterior achaetous segments	28
25 Parapodial lappets well developed, posterior part of the body finishing truncated	26
Parapodial lappets little developed, posterior part of the body tapered to the pygidium	27
26 Lateral lappets well developed, pygidium cylindrical	<i>T. kerguelensis</i>
Laterals lappets absent, a pair of dorsal anal cirri at the end of the anal cylinder	<i>T. kerguelensis gravieri</i>
27 Setigers number 23-26, posterior margin of abdominal segment smooth, not scalloped, pygidium ovoid	<i>T. forbesii</i>
Setigers number 26-29, posterior margin of abdominal undulate or serrulate, pygidium cylindrical	<i>T. forbesii intermedia</i>
28 Parapodial lappets little developed, pygidial knob pigmented, 23 setigers, 28 segments	<i>T. horsti</i>
Parapodial lappets developed, pygidium not pigmented	29
29 Branchiae number ≥ 20 , 27 segments, 24 setigers.....	<i>T. chiloensis</i>
Branchiae number ≤ 20 , 29 segments	30
30 Setigers number 23-25	<i>T. brevis</i>
Setigers number 27	<i>T. chinensis</i>

BIOGEOGRAPHICAL DISTRIBUTION

Table 1 summarizes available data of species distribution. Only two species occur in Arctic Ocean; Antarctic Ocean is richer with eight taxa. *T. antarctica* is present in the far-south (South Georgia) of the Atlantic Ocean. Ten species are present in the Atlantic Ocean, two of which are restricted to the northern part, five to the southern part

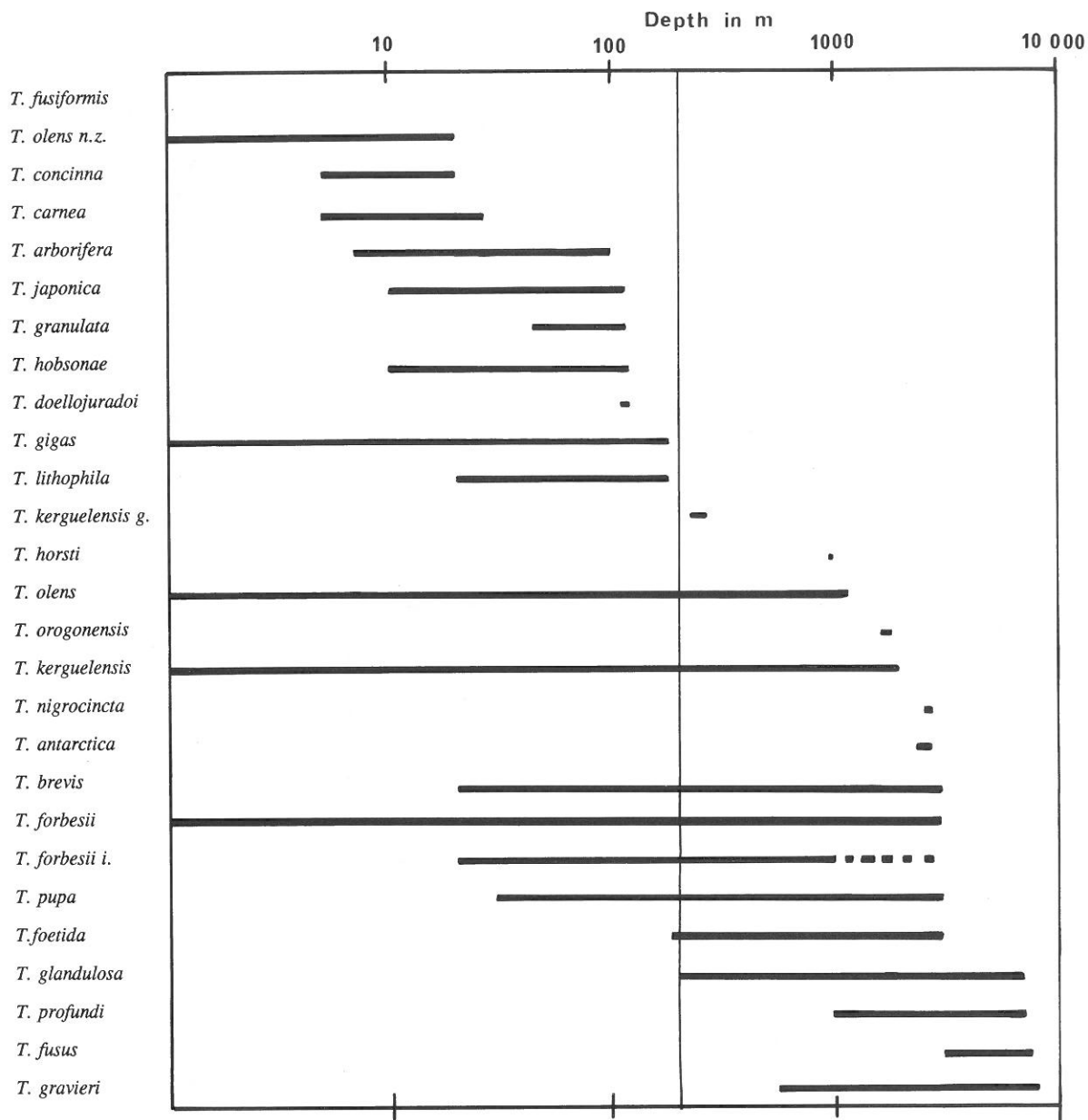
and three have an extended distribution. Twenty-one taxa are present in the Pacific Ocean, 13 are restricted to the north, with *T. arborifera* found in the Gulf of Bengal which is the single species collected in the Indian Ocean. Six species are known to be only from the south Pacific Ocean. Eight species have a large biogeographical distribution: *T. glandulosa*, *T. forbesii*, *T. fusus*, *T. gravieri*, *T. japonica*, *T. kerguelensis*, *T. olens*, and *T. profundus*.

TABLE 1. — Biogeographical distribution of *Travisia* species from the world's oceans.

	Arctic	Atlantic	Patagonian	Pacific	Antarctic
Shelf	<i>brevis</i> <i>forbesii</i>				<i>kerguelensis</i> , <i>olens</i> , <i>lithophila</i>
Boreal NE		<i>forbesii</i>		<i>brevis</i> , <i>forbesii</i> , <i>gigas</i> , <i>japonica</i> , <i>pupa</i>	
Boreal NW		<i>carnea</i> , <i>forbesii</i>		<i>brevis</i> , <i>forbesii</i> , <i>japonica</i>	
Lusitanic		<i>forbesii</i>			
W. Tropical and Indian				<i>arborifera</i> , <i>chinensis</i> , <i>japonica</i>	
Caribbean		<i>hobsonae</i>		<i>fusiformis</i> , <i>gigas</i> , <i>granulata</i>	
S. America tropical		<i>forbesii</i> <i>doellojuradoi</i>			
S. Africa tropical		<i>concinna</i> <i>forbesii</i>			
Tasmania N.Z.				<i>kerguelensis</i> , <i>lithophila</i> , <i>olens</i> , <i>olens n.z.</i>	
Araucanic			<i>chiloensis</i> <i>kerguelensis</i> , <i>olens</i> , <i>olens n.z.</i>	<i>elongata</i>	
Bathyal Abyssal	<i>forbesii</i>				<i>glandulosa</i> , <i>antarctica</i> <i>kerguelensis</i> , <i>k. gravieri</i> , <i>nigrocincta</i> , <i>olens</i> , <i>profundi</i> ,
North		<i>glandulosa</i> , <i>forbesii</i> , <i>gravieri</i> ,		<i>glandulosa</i> , <i>forbesii</i> , <i>profundi</i> , <i>pupa</i>	
East		<i>glandulosa</i> , <i>gravieri</i>		<i>glandulosa</i> , <i>brevis</i> , <i>foetida</i> , <i>forbesii</i> , <i>fuscus</i> , <i>orogonensis</i> <i>profundi</i> , <i>pupa</i>	
West		<i>antarctica</i> , <i>forbesii</i> , <i>gravieri</i>		<i>glandulosa f. intermedia</i> <i>fuscus</i> , <i>horsti</i> , <i>olens</i> , <i>profundi</i> , <i>pupa</i>	

BATHYMETRIC DISTRIBUTION

Three species *T. chiloensis*, *T. chinensis* and *T. elongata* were described without indication of original depth, and were probably littoral species. Among the other 27 taxa, 16 are present in the bathyal and/or the abyssal depths and 10 are exclusively bathyo-abyssal (Fig. 1). Eighteen species are found on the continental shelf among which only five species are collected at depths less than 100 m.

FIG. 1. — Bathymetric distribution of *Travisia* species from the world's oceans.

ECOLOGICAL AND BIOLOGICAL DISTRIBUTION

The data on the ecology of the species are rarely reported and therefore the ecological and biological data are incomplete. Most of the deeper species are found in bathyal and abyssal mud. The littoral species are found especially in muddy and fine sand. *T. foetida* inhabits essentially clean sands in low intertidal and in the upper part of the subtidal. However, this species has been found also in many different types of soft-bottom substrates. Due to its widespread distribution both geographical and bathymetric, *T. forbesii* appears to be ubiquitous. This ubiquity may be the result of the presence of a complex of species. The principally northern species *T. forbesi* may have a counterpart in the southern hemisphere with *T. kerguelensis* and *T. olens* and their sub-species.

Travisia are considered non-selective deposit-feeders. In the intertidal sand at Tampa Bay, Florida, specimens of *Travisia hobsonae* had only sand particles in their gut with no particles finer than 100 μm ; grains as large as 475 μm were removed with a median size of 230 μm (DAUER, 1980). The low level of food specialization in adults contrasts sharply with the high level of precision in the selection of substrata by juveniles (RETIÈRE, 1971, 1972).

Travisia forbesi lives 3.5 years at Dinard (English Channel); the spawning occurs at the end of the autumn and during the winter; development is direct without larval dispersion (RETIÈRE, 1971, 1972). *T. hobsonae* reproduces the year round in Tampa Bay (DAUER, 1980); its densities could reach an annual average of 1,100 m^{-2} at certain stations.

DISCUSSION

This paper is a first step toward the study of Traviinae and to the knowledge of the Opheliidae family. The sub-family Traviinae is the most plesiomorph (BELLAN *et al.*, 1990) and is well defined in relation to the two other sub-families. This paper proposes to bring together all the species of this sub-family into the one genus *Travisia* Johnston, 1840. The examination of available types has allowed us to place into synonymy *Kesun abyssorum* Monro, 1930 with *Travisia glandulosa* McIntosh, 1879, and *T. parva* Day, 1973 with *T. carnea* Verrill, 1873. Five species *T. chiloensis*, *T. chinensis*, *T. concinna*, *T. elongata* and *T. horsti* which have not (or rarely) been found since their description, remain doubtful and must be re-examined. Many characters should be used in defining each species: color and shape of live specimens; presence, shape, and variability of posterior lateral crenulations and parapodial lappets; number and variability of number of segments and setigers; number of branchiae; distribution of pustulae on the body; shape of the pygidium and pygidial papillae. The variability of the number of setigers, segments, and branchiae must be defined using a large number of specimens of each species. This work would allowed in a further step to study the phenetic and the phylogenetic relationship between the species. However, genetical studies must be established: 1) the real extended distribution of *T. forbesii* and *T. forbesii intermedia* (northern species); *T. forbesii* may be a complex with slight morphological differences; 2) the genetical distance and variability of the southern species and their sub-species: *T. kerguelensis*, *T. kerguelensis gravieri*, *T. olens* and *T. olens novae zealandiae*. These four taxa are distinguishable essentially by the number of segments and setigers, so they show a continuum between *T. kerguelensis* with a number of segments which could be reduced to 23 and *T. olens novae zealandiae* which a number of segments reaching 40. *T. kerguelensis* is known to show a great variability of papillation in the posterior segments (MONRO, 1930).

It is clear that the data on ecological and biological features are insufficient. Biological data are limited to *T. forbesii* and *T. hobsonae*. Such studies must be extended to other species and populations. In the past few years several works on *Ophelia*, such as those of RISER (1987) and HARRIS (1991) have demonstrated that biological (type of development) and ecological data (habitat) could be good criteria to ascertain on the validity of a particular species in this family.

Travisia is typically a deep water Pacific genus. Bathymetric distributions of *Travisia* and *Ophelia* (BELLAN & DAUVIN, 1991) show that *Ophelia* occurs preferentially in shallow waters and in the Atlantic whereas *Travisia* species dominate in the bathyal and abyssal depths in the Pacific. This indicates that the speciation of these two genera could be parallel. In Ampeliscidae (Amphipoda), another marine diversified family, DAUVIN & BELLAN-SANTINI (1990) have also distinguished two distribution schemes with *Ampelisca* in shallow water and *Haploops* in continental and bathyal depths.

New data are need before elucidating the evolution of the genus. Future works and prospects on *Travisia* genus, but also on other genera of Opheliidae may reveal correlations between species, phyletic, bathymetric and biogeographic features.

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REFERENCES

- AMOUREUX, L., 1971. — Annélides Polychètes capturés au large de la côte d'Arcachon. Inventaire taxonomique. *Bull. Soc. Linn. Bordeaux*, 1 : 147-164.
- AMOUREUX, L., 1982. — Annélides Polychètes recueillies sur la pente continentale de la Bretagne à l'Irlande, campagne 1973 de la "Thalassa" (suite et fin) avec la description de quatre nouvelles espèces pour la science. II. Inventaire taxonomique annoté de toutes les Polychètes Sédentaires. *Cah. Biol. mar.*, 23 : 179-214.
- ANNEKOVA, N., 1937. — The polychaete fauna of the northern part of the Japan Sea [in russian]. *Issledovaniya Fauny Morei. SSSR.*, 23 : 139-316.
- ANNEKOVA, N., 1938. — Polychaeta of the North Japan Sea and their horizontal and vertical distribution. Hydrobiol. Exped. U.S.S.R. in 1934 to the Japanese Sea [in russian]. *Trudy D.-V. Filial Akad. Nauk.*, 1 : 81-230.
- APPY, T.D., LINKLETTER, L.E. & DADSWELL, M.J., 1980. — A guide to the Marine Flora and Fauna of the bay of Fundy : Annelida: Polychaeta. *Fish. & Mar. Service Tech. Rep.*, 920 : 1-124.
- AUGENER, H., 1922. — Revision der australischen Polychaeten-Typen von Kinberg. *Arkiv für Zool.*, 14 : 1-42.
- AUGENER, H., 1923. — Polychaeten von den Auckland und Campbell-Inseln. *Vidensk. Medd. naturh. Foren. København*, 75 : 1-115.
- AUGENER, H., 1932. — *Antarktische und Antiboreale polychaeten nebst einer Hirudinae*. Scientific Results of the Norwegian Antarctic Expedition 1927-28. Norske Videnskaps Akad. Oslo, 86 pp.
- AVERINCEV, V.G., 1974. — The polychaetous annelids of the abyssal and bathyal zones of the Scotian arc based on the 11 th cruise of R/V "Akademik Kurchatov" [in russian]. *Trudy Inst. Okeanol. Moscou*, 98 : 213-227.
- AVERINCEV, V.G., 1977. — Explorations of the fauna of the seas. Biocoenoses of the shelf of Franz Josef Land and the fauna of adjacent waters [in russian]. *Acad. Sci. U.S.S.R.*, 14 : 140-184.
- AVERINCEV, V.G., 1982. — Seasonal variations in the sublittoral polychaetes fauna (Polychaeta) of the Davis Sea [in russian]. *Issledovaniya Fauny Morei, SSSR*, 28 : 4-70.
- BANSE, K. & HOBSON, K.B., 1968. — Benthic polychaetes from Puget Sound, Washington, with remarks on four others species. *Proc. U.S. Nat. Hist. Mus.* 125, 3667: 1-53.
- BELLAN, G., BELLAN-SANTINI, D. & DAUVIN, J.C., 1990. — Phénétique et phylogénie des Opheliidae (Annélides Polychètes). *C. R. Acad. Sci. Paris*, 310, sér. III : 175-181.
- BELLAN, G. & DAUVIN, J.C., 1991. — Phenetic and biogeographic relationships in *Ophelia* (Polychaeta, Opheliidea). *Bull. Mar. Sci.*, 48 : 544-558.
- BELLAN-SANTINI, D., DAUVIN, J.C. & BELLAN, G., 1992. — Approche phénétique et phylogénétique des *Ophelia* (Annélides Polychètes) de Méditerranée occidentale. *Bull. Inst. Océanogr. Monaco*, n° spéc. 9 : 67-81.
- BENHAM, W.B., 1927. — Polychaeta. British Antarctic Terra Nova Expedition 1910. *Nat. Hist. Rep., Zoology*, 7 : 47-182.
- BENHAM, W.B., 1950. — Polychaeta of the Auckland and Campbell Islands. *Bull. Cap. Exped. Ser. Wellington N. Z.*, 10 : 1-26.
- BERKELEY, C., 1966. — Records of some species of Polychaeta new to British Columbia and of extension in distribution of some others. *Can. J. Zool.*, 44 : 839-849.
- BERKELEY, C., 1968. — A checklist of Polychaeta recorded from the British Columbia since 1923, with references to name changes descriptions, and synonymies II. Sedentaria. *Can. J. Zool.*, 46: 557-567.

- BERKELEY, E. & BERKELEY, C., 1941. — On a collection of Polychaeta from southern California. *Bull. S. California Acad. Sci.*, **40** : 16-80.
- BERKELEY, E. & BERKELEY, C., 1942. — North Pacific Polychaeta from the west coast of Vancouver Island, Alaska and Bering Sea. *Can. Jour. Res. Ottawa*, **20** : 183-208.
- BERKELEY, E. & BERKELEY, C., 1952. — 9. Annelida, Polychaeta Sedentaria. *Canadian Pacific Fauna, Fish Res. Bd Canada*, **9b** : 1-139.
- BERKELEY, E. & BERKELEY, C., 1962. — Polychaeta from the British Columbia with a note on some Western Canadian artie forms. *Can. J. Zool.*, **40** : 571-577.
- BUZHINSKAYA, G.N., 1985. — Polychaeta of the shelf off south Sakhalin and their ecology [in russian]. *Issledovaniya Fauny Morei, SSSR*, **30** : 72-224.
- CABIOCH, L., L'HARDY, J.P. & RULLIER, F., 1968. — Inventaire de la faune marine de Roscoff. Annélides. *Trav. Stat. Biol. Roscoff*, **17** : 1-95.
- CHAMBERLIN, R.V., 1919. — The Annelida Polychaeta. *Mem. Mus. Comp. Zool. Harvard.*, **48** : 1-514.
- CAULLERY, M., 1944. — Polychètes sédentaires de l'expédition du Siboga : Ariciidae, Spionidae, Chaetopteridae, Chloeraemidae, Opheliidae, Oweniidae, Sabellariidae, Sternaspidae, Amphictenidae, Ampharetidae, Terebellidae. *Siboga Exped.*, **24** : 1-204.
- CHLEBOVITSCH, V.V., 1961. — Polychètes littorales des Kouriles [in russian]. *Rech. Mers Lointaines de L'Ouest de l'U.R.S.S.*, **7** : 151-260.
- DAUER, D.M., 1980. — Population dynamics of the polychaetous Annelids of an intertidal habitat in the upper old Tampa Bay, Florida. *Int. revue ges. Hydrobiol.*, **65** : 461-487.
- DAUVIN, J.C. & BELLAN-SANTINI, D., 1990. — An overview of the Amphipod genus *Haploops* (Ampeliscidae). *J. mar. biol. Ass. U.K.*, **70** : 887-903.
- DAY, J.H., 1961. — The polychaete fauna of South Africa. Part 6. *J. Linn. Soc. London*, **4**, 469-560.
- DAY, J.H., 1967. — *A monograph on the Polychaeta of Southern Africa. Part II. Sedentaria*. British Museum Natural History Publication, London, 878 pp.
- DAY, J.H., 1973. — New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Tech. Rep. NMFS*, **375** : 1-140.
- DAY, J.D. & HUTCHINGS, P., 1979. — An annotated checklist of Australian and New Zealand polychaeta, Archiannelida and Myzostomida. *Rec. Austr. Mus.*, **32** : 80-161.
- EHLERS, E., 1887. — Report on the annelids of the dredging expedition of the U.S. coast survey Steamer Blake. *Mem. Mus. Comp. Zool.*, **15** : 1-335.
- EHLERS, E., 1897. — *Polychaeten*. Hamburger Magellhaenische Sammelreise, Hamburg, 148 pp.
- EHLERS, E., 1901. — *Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch*. Festschrift zur Feier des Hunderfünfzigjährigen Bestehens des königlichen Gesellschaft der Wissenschaften zu Göttingen (Abh. Math.-Phys.). Berlin, 232 pp.
- EHLERS, E., 1907. — Neusselandische Anneliden. II. *K. Ges. wiss. Göttingen, Math-Phys. Kl., Abh., n. Folge*, **5** : 1-31.
- EHLERS, E., 1908. — *Wissenschaftliche Ergebnisse der deutschen Tiefsee-expedition auf dem Dampfer Valdivia 1898-1899. Im Auftrage des Reichsamtes des Innern, herausgegeben von Carl Chun, Professor der zoologie in Leipzig, Leiter der Expedition*, 16, 1. *Die Bodensässigen Anneliden aus den Sammlungen der deutschen Tiefsee-Expedition*. Jena, Gustav Fischer, 168 pp.
- EHLERS, E., 1912. — Polychaeta. National Antarctic Expedition, 1901-1904. *Nat. Hist.*, **6** (Zool.) : 1-32.
- EHLERS, E., 1913. — Die Polychaeten Sammlungen des deutschen Südpolar Expedition 1901-1903. *Deutsche Südpolar Exped.*, **13** : 397-598.
- ELIASON, A., 1962. — Undersökningar över Öresund. 41. Weitere Untersuchungen über die Polychaeten -fauna des Öresunds. *Acta. Univ. Lun.*, **2**, 16 : 1-103.
- FAUCHALD, K., 1972. — Benthic Polychaetous annelids from the deep water off western Mexico and adjacent areas in the eastern pacific ocean. *Allan Hancock Monogr. Mar. Biol.*, **7** : 1-575.

- FAUCHALD, K., 1977. — The polychaete worms. Definitions and keys to the Orders, Families and genera. *Nat. Hist. Mus. Los Angeles county, Sci., ser.* **28** : 1-190.
- FAUCHALD, K. & HANCOCK, D.R., 1981. — Deep-water Polychaeta from a transect off central Oregon. *Monogr. Ser. Allan Hancock Found.*, **11** : 1-73.
- FAUVEL, P., 1914. — Annélides Polychètes non pélagiques provenant des campagnes de l'Hirondelle et de la Princesse Alice (1885-1910). *Res. Camp. Sci. accomplies sur son Yacht par Albert Ier*, **46** : 1-432.
- FAUVEL, P., 1925. — Sur les Ophéliens des côtes de France. *Bull. Soc. Zool. France*, **50** : 77-88.
- FAUVEL, P., 1932. — Annelida Polychaeta of the Indian Museum, Calcutta. *Mem. Indian Mus.*, **12** : 1-262.
- FAUVEL, P., 1933. — Annélides polychètes du Golfe du Pei Tcheu Ly de la collection du Musée Hoang ho Pai ho, récoltées par le R.P. Leroy, S.J., et le R. P. Licent, S.J. *Publ. Musée Hoang ho Pai ho Tien-Tsin*, **15** : 1-67.
- FAUVEL, P., 1936. — Annélides Polychètes du Japon. *Mem. Coll. Sci. Kyoto Imperial Univ., Ser. 13*, **12** : 41-92.
- FAUVEL, P., 1941. — Annélides Polychètes de la mission du Cap Horn (1882-1883). *Bull. Mus. natl Hist. nat. Paris, n.s.*, **13** : 272-298.
- FAUVEL, P., 1943. — Annélides Polychètes de Californie recueillies par L. Diguët. *Mém. Mus. nat. Hist. nat., n.s.*, **18** : 1-32.
- FAUVEL, P., 1953. — *The fauna of India*. The Indian Press Ltd Allahabad, 507 pp.
- FOURNIER, J.A. & LEVINGS, C.D., 1982. — Polychaetes recorded near two pulp mills on the coast of Northern British Columbia: a preliminary taxonomy and ecological account. *Syllogeus*, **40** : 1-91.
- FUJIWARA, T., 1933. — On a new species of Japanese polychaeta *Travisia japonica* sp. nov. *J. Sci. Hiroshima Univ. Zool.*, **2** : 91-103.
- GLÉMAREC, M., 1969. — *Les peuplements benthiques du plateau continental Nord-Gascogne*. Thèse Doctorat d'Etat, Université de Brest, 167 pp.
- GRUBE, E., 1866. — Neue Anneliden aus den Gattungen *Eunice*, *Hesione*, *Lamprophaes* und *Travisia*. *Jahresber. Schles. Gesells. in Breslau*, **44** : 64-66.
- GRUBE, E., 1869. — Familie der Opheliaceen. *Jahresber. Schles. Gesells. Vaterl. Breslau*, **45** : 59-68.
- HAMOND, R., 1966. — The Polychaeta of the coast of Norfolk. *Cah. Biol. mar.*, **7** : 383-436.
- HARRIS, T., 1991. — The occurrence of *Ophelia bicornis* (Polychaeta) in and near the estuary of the River, Exe, Devon. *J. mar. Biol. Ass. U.K.*, **71** : 391-402.
- HARTMAN, O., 1938. — Description of new species and new generic records of polychaetous annelids from California of the families Glyceridae, Eunicidae, Stauroneridae and Opheliidae. *Calif. Public. Zool.*, **43** : 93-111.
- HARTMAN, O., 1948. — The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Ark. Zool. Stockholm*, **42** : 1-137.
- HARTMAN, O., 1952. — The marine annelids of the United States Navy Antarctic Expedition, 1947-48. *J. Wash. Acad. Sci.*, **42** : 231-237.
- HARTMAN, O., 1953. — Non pelagic Polychaeta of the Swedish Antarctic Expedition 1901-1903. *Further Zool. Res. of the Swedish Antarctic Expedition 1901-1903, Stockholm*, **4**, 11: 1-83.
- HARTMAN, O., 1959. — Catalogue of the Polychaetous annelids of the world. *Allan Hancock Found. Occ. Papers*, **23** : 1-628.
- HARTMAN, O., 1961. — Polychaetous Annelids from California. *Allan Hancock Pacif. Exped.*, **25** : 1-226.
- HARTMAN, O., 1963. — Submarine canyons of southern California. Part III. Systematics: Polychaetes. *Allan Hancock Pacific Exped.*, **27** : 1-93.
- HARTMAN, O., 1965a. — Deep-water benthic Polychaetous Annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Found. Occas. Pap.*, **28** : 1-378.
- HARTMAN, O., 1965b. — Benthic biology of the mainland of California. Sections on Polychaetes. In: *An Oceanographic and Biological Survey of the Southern California Mainland Shelf*. Publication n° 27. State Water quality Control Board, Sacramento, California : 1-232.

- HARTMAN, O., 1966a. — Quantitative survey of the benthos of San Pedro Basin, Southern California. Part 2. Final results and conclusions. *Allan Hancock Pacific Exped.*, **19** : 187-456.
- HARTMAN, O., 1966b. — Polychaeta Myzostomidae and Sedentaria of Antarctica. *Antarctic Res. Ser.*, **7** : 1-158.
- HARTMAN, O., 1967. — Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from the antarctic seas. *Allan Hancock Monogr. Mar. Biol.*, **2** : 1-387.
- HARTMAN, O., 1969. — *Atlas of sedentariate polychaetes annelids from California*. Allan Hancock Foundation, University of Southern California, 812 pp.
- HARTMAN, O., 1978. — Polychaeta from the Weddell Sea quadrant, Antarctica. *Antarctic Res. Ser.*, **26** : 124-223.
- HARTMAN, O. & FAUCHALD, K., 1971. — Deep-water benthic Polychaetous Annelids off New England to Bermuda and other North Atlantic areas. Part II. *Allan Hancock Monogr. Mar. Biol.*, **6** : 1-327.
- HARTMANN-SCHRÖDER, G., 1971. — Annelida, Borstenwürmer, Polychaeta. *Tierwelt Deutschlands*, **58** : 1-594.
- HARTMANN-SCHRÖDER, G. & HARTMANN, G., 1980. — Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. teil 4. Die Polychaeten der tropischen Nordwestküste (zwischen Port Samson im Norden und Exmouth im Süden). *Mitt. hamb. zool. Mus. Inst.*, **77** : 41-110.
- HARTMANN-SCHRÖDER, G., 1986. — Die Polychaeten der 56 Reise der "Meteor" zu den South Shetland-Inseln (Antarktis). *Mitt. hamb. zool. Mus. Inst.*, **83** : 71-100.
- HARTMANN-SCHRÖDER, G. & ROSENFELDT, P., 1989. — Die Polychaeten der "Polarstern" -Reise Ant III/2 in die Antarktis 1984. Teil 2: Cirratulidae bis Serpulidae. *Mitt. hamb. zool. Mus. Inst.*, **86** : 65-106.
- HOBSON, K.D. & BANSE, K., 1981. — Sedentariate and Archiannelid polychaetes of British Columbia and Washington. *Can. Bull. Fish. Aquat. Sci.*, **209** : 1-144.
- HOLTJE, T., 1977. — The Polychaetous annelids of Trondheimsfjorden, Norway. *Gunneria*, **29** : 1-64.
- HUTCHINGS, P. & MURRAY, A., 1984. — Taxonomy of Polychaetes from Hawkesbury River and the Southern Estuaries of New South Wales, Australia. *Rec. Austr. Mus.*, **36**, suppl. 3 : 1-119.
- IMAJIMA, M., 1961. — Polychaetous annelids collected off the west coasts of Kamchatka. 1. Notes on species in the collections 1957-58. *Publ. Seto Mar. Biol. Lab.*, **9** : 81-102.
- IMAJIMA, M., 1963. — Polychaetous annelids collected off the west coast of Kamchatka. 2. Notes on species found in the collection of 1959. *Publ. Seto Mar. Biol. Lab.*, **11** : 345-372.
- IMAJIMA, M., 1964. — Benthic Polychaetes collected by the second cruise of the Japanese Expedition of deep seas (JEDS-2). *Bull. natn. Sci. Mus. Tokyo*, **7** : 235-254.
- IMAJIMA, M. & HARTMAN, O., 1964. — The Polychaetous annelids of Japan. *Allan Hancock Found. Occas. Pap.*, **26** : 1-452.
- JONHSTON, G., 1840. — British Annelids. *Ann. Mag. nat. Hist.*, ser. 1, **4** : 368-375.
- KINBERG, J.G.H., 1866. — Annulata nova. *Oefv. Svenska Vetensk. Akad. Förh.*, **22** : 239-258.
- KINBERG, J.G.H., 1910. — *Konglia Svenska Fregatten Eugenie's Resa omkring jorden under befäl af C.A. Virgin åren 1851-853. Vetenskapliga Iakttagelser på Konung Oscar den Förstes befallning utgifna delen. Zoologi. 3. Annulater*. Uppsala and Stockholm, Almqvist and Wicksells, 78 pp.
- KIRKEGAARD, J.B., 1956. — Benthic Polychaeta from depths exceeding 6,000 m. *Galathea Rep.*, **2** : 63-78.
- KIRKEGAARD, J.B., 1969. — A quantitative investigation of the central North Sea Polychaete. *Spolia*, **29** : 1-285.
- KIRKEGAARD, J.B., 1980. — Abyssal benthic polychaetes from the northeast Atlantic ocean southwest of the British Isles. *Sireenstrupia*, **6** : 81-98.
- KNOX, G.A., 1962. — Antarctic Polychaetes from Mawson. Mac Robertson Land. *Trans. Roy. Soc. Nat. New Zealand, Zool.*, **1** : 343-348.
- KUDENOV, J.D., 1975. — Sedentary Polychaeta from the Gulf of California, Mexico. *J. Nat. Hist.*, **9** : 205-231.
- KÜKENTHAL, W., 1887. — Die Opheliaceen der Expedition der "Vettore Pisani". *Jena. Z. Naturw.*, **21** : 361-373.
- LEVENSTEIN, P.P., 1960. — The quantitative distribution of the Polychaeta in the north western Bering Sea [in russian]. *Trudy Inst. Okeanol., Moscou*, **44** : 104-122.

- LEVENSTEIN, P.P., 1961a. — The quantitative distribution of the Polychaeta in the north Pacific [in russian]. *Trudy Inst. Okeanol., Moscou*, **45** : 214-222.
- LEVENSTEIN, P.P., 1961b. — Polychaeta in the deep sea area of the Bering Sea [in russian]. *Trudy Inst. Okeanol., Moscou*, **46** : 214-222.
- LEVENSTEIN, P.P., 1961c. — New data on the Annelida Polychaeta from the deep waters of Java [in russian]. *Okeanol.* **1** : 136-139.
- LEVENSTEIN P.P., 1966. — Polychaeta of the Bering Sea [in russian]. *Trudy Inst. Okeanol., Moscou*, **81** : 3-131.
- LEVENSTEIN, P.P., 1970. — Ecology and zoogeography of some Pacific Polychaeta of the family Opheliidae. *Trudy Inst. Okeanol., Moscou*, **88** : 213-226.
- LEVENSTEIN, P.P., 1971/72. — Ecology and Zoogeography of some Polychaeta representatives of the abyssal Pacific. *Proc. R.S.E. (B)*, **73**, 18 : 171-181.
- LEVENSTEIN, P.P., 1975. — The Polychaetous annelids of the deep sea trenches of the Atlantic Sector of the Antarctic ocean [in russian]. *Tans. P.P. Shirshov Inst. Okeanol.*, **103** : 119-142.
- LEVENSTEIN, P.P., 1978. — The Polychaetous annelids from the deep sea pacific antarctic ocean [in russian]. *Trudy Inst. Okeanol., Moscou*, **113** : 73-87.
- LOI, T.N., 1980. — Catalogue of the types of polychaete species erected by J. Percy Moore. *Proc. Acad. Nat. Sci. Philadelphia*, **132** : 121-149.
- MCINTOSH, W.C., 1879. — On the Annelida obtained during the cruise H.M.S. "Valorous" to Davis Stait in 1875. *Trans. Linn. Soc. London, n.s.*, **1** : 499-511.
- MCINTOSH, W.C., 1885. — Report on the Annelida Polychaeta collected by H.M.S. "Challenger" during the years 1873-1876. *Challenger Rep.*, **12** : 1-554.
- MCINTOSH, W.C., 1908a. — On the same Families of Annelids in the "Porcupine" expeditions of 1869 and 1870, n° 29. *Ann. Mag. Nat. Hist.*, ser 8, **1** : 383-391.
- MCINTOSH, W.C., 1908b. — Notes from the Gatty Marine Laboratory, St Andrews, 29. *Ann. Mag. Nat. Hist. London, ser. 8*, **1** : 373-387.
- MCINTOSH, W.C., 1915. — *The British Marine Annelids. Polychaeta. Opheliidae to Ammocharidae*. Vol. **3**, Part 1: 1-368.
- MOORE, J.P., 1906. — Additional new species of Polychaete from the north Pacific. *Proc. Acad. Nat. Sci. Phil.*, **58** : 217-260.
- MOORE, J.P., 1923. — The Polychaetous annelids dredged by the USS Albatross off the coast of Southern California in 1904. IV Spionidae to Sabellidae. *Proc. Acad. Nat. Sci. Philadel.*, **75** : 179-259.
- MOORE, C.C.A., 1930. — Polychaete worms. *Discovery Rep., Cambridge*, **2** : 1-222.
- MOORE, C.C.A., 1934. — On a collection of Polychaeta from the coast of China. *Ann. Mag. nat. Hist.*, ser. 10, **13** : 353-380.
- MOORE, C.C.A., 1936. — Polychaete worm. II. *Discovery Rep., Cambridge*, **12** : 59-198.
- MOORE, C.C.A., 1939. — Polychaeta. British Antarctic Research Expedition, 1929-1931. *Adelaide, Australia. Rep., ser.B (Zoology and Botany)*, **4** : 89-156.
- PETTIBONE, M.H., 1954. — Marine Polychaeta worms from Point Barrow, Alaska, with additional record from the North Atlantic and North Pacific. *Proc. U.S. Nat. Hist. Mus.*, **103** (3324) : 203-356.
- PETTIBONE, M.H., 1956. — Marine Polychaete worms from Labrador. *Proc. U.S. Nat. Hist. Mus.*, **105** (3361) : 531-584.
- RATHKE, H., 1843. — Beiträge zur Fauna Norwegens. *Nova. Acta Acad. Leop. Carol. Nat. Cur. Halle*, **20** : 1-264.
- REISH, D.J., 1965. — Benthic Polychaetous Annelids from Bering Chukchi and Beaufort Seas. *Proc. U.S. Nat. Hist. Mus.*, **117** (3511) : 131-158.
- REISH, D.J., 1968. — A biological survey of Bahia de Los Angeles: gulf of California. Mexico II. Benthic Polychaetous annelids. *Trans. San Diego Soc. Nat. Hist.*, **15** : 67-106.
- RETIÈRE, C., 1968. — Contribution à l'étude écologique de la macrofaune annélide de la plage de Lancieux (Côtes du Nord). *Bull. Mar. Lab. Dinard*, **1** : 1-59.

- RETIÈRE, C., 1971. — Données sur l'écologie de la Polychète *Travisia forbesii* Johnston 1840 (Opheliidae) dans la région de Dinard : mise en évidence du cycle biologique. *C. R. Acad. Sci. Paris*, **272**, sér D : 3075-3078.
- RETIÈRE, C., 1972. — Structure et dynamique d'une population de *Travisia forbesii* Johnston 1840 (Opheliidae) dans la région de Dinard. *C. R. Acad. Sci. Paris*, **275**, sér D : 1543-1546.
- RIOJA, E., 1944. — Estudios anelidológicos. II. Estudios de algunos poliquetos del Museo Argentino de ciencias naturales. *An. Inst. Biol. Univ. Mex.*, **15** : 115-138.
- RIOJA, E., 1946. — Estudios de algunos poliquetos del Museo Argentino de ciencias naturales. *An. Mus. Argent. B. Aires*, **42** : 39-58.
- RISER, N.W., 1987. — Observations on the genus *Ophelia* (Polychaeta Opheliidae) with the description of a new species. *Ophelia*, **28** : 11-29.
- ROZBACZYLO, N., 1985. — Los Anelidos poliquetos de Chile. *Monografías Biológicas*, **3** : 1-284.
- SAINT-JOSEPH, A. de, 1898. — Les Annélides polychètes des côtes de France (Manche et Océan). *Ann. Sci. Nat. Paris*, sér. 8, **5** : 209-464.
- SANTOS, S., 1977. — A new species of *Travisia* (Polychaeta, Opheliidae) from Tampa Bay, Florida. *Proc. Biol. Soc. Wash.*, **89** (49) : 559-564.
- STÖP-BOWITZ, C., 1945. — Les Ophéliens Norvégiens. *Medd. zool. Mus. Oslo*, **52** : 1-61.
- STÖP-BOWITZ, C., 1948. — Sur les Polychètes arctiques des Familles Glycériens, des Ophéliens, des Scalibrégmiens et des Flabelligériens. *Tromsø Mus. Arshefter*, **66** : 1-58.
- TREADWELL, A.L., 1914. — Polychaetous annelids of the Pacific coast in the collection of the Zoological Museum of the University of California. *Univ. Calif. Publ. Zool.*, **13** : 175-234.
- UEBELACKER, J.M., 1984. — Chapter 17. Opheliidae. In : J.M. UEBELACKER & P.G. JOHNSON (eds.), *Taxonomic guide to the polychaetes of the northern Gulf of Mexico*. Vol. III. Bary A. VITTOR & Associates, Inc., Mobile, Alabama **7** : 1-15.
- UCHIDA, H., 1967. — Polychaetous annelids from Shakotan. (Hokkaido). I. The collection in 1967. *J. Fac. Sci. Hokkaido Univ. (Zool.)*, **16** : 595-612.
- USCHAKOV, P.V., 1955. — Polychaeta of the Far Eastern seas of the USSR [In Russian]. *Akad. Nauk SSSR, Zool. Inst., Opred. po faune SSSR*, **56** : 1-445.
- VERRILL, A.E., 1873. — Report upon invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Rep. U.S. Commissioner Fish.*, 1871-1872 : 295-778.
- WESENBERG-LUND, E., 1950. — Polychaeta. *Danish Ingolf Exped.*, **4**, 14 : 1-92.
- WESENBERG-LUND, E., 1951. — Polychaeta. *The Zoology of Iceland*, **2**, 19 : 1-182.
- WILEY, E.O., 1981. — *Phylogenetics. The theory and practice of Phylogenetic Systematics*. J. Wiley and Sons, New York, 439 pp.
- WOLFF, W.J., 1973. — The estuary as a habitat : an analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Sheldt. *Zool. Verhandl. Leiden*, **126** : 1-242.