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Systematics, ecology and biogeographical relationships in the sub-family Travisiinae (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 Travisiinae. The object of the current paper is to offer a contribution to the knowledge of the sub-family Travisiinae 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. profundi.* A study of the relationship between species and biogeographical distribution is given.

RÉSUMÉ

Systématique, écologie et relations biogéographiques dans la sous-famille des Travisiinae (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 Travisiinae. 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 Travisiinae. 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

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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. profundi.* 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 Travisiinae. This last sub-family seems particulary 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 Travisiinae, 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 TRAVISIINAE

The sub-family Travisiinae 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 serratulate-ciliate setae. However, these authors pointed out that these characters needed to be confirmed. A certain number of Travisiinae belonging to genus *Kesun* and *Travisia* have been also described with hispid and/or serratulated 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 Travisiinae 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 profundi* and from many other species of the genus. The absence of epipodial pads is also not a unique feature either. This leaves only one unequivoqual 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 K*esun* 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 Travisiinae with a supplementary character: the presence of pustulae or similar structure on the body.

The fact that remains only one genus *Travisia* in the Travisiinae 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 (Travisiinae) 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 Travisiinae
- Sub-family Opheliinae
- Sub-family Ophelininae

This classification regards the very strong differenciation between the Travisiinae 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, Massachussets to long Island, Arctic Alaska. 5-35 m. (2)

• *T. chiloensis* 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, Perou, 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 Amazone, 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* Annekova, 1937 as a *T. forbesi* subsp. *intermedia* (Annekova, 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 Archipelo, 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. (i)
• *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. profundi* 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 Bassin), 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. profundi* where they are present from setiger 3. Unusual lobes or papillae are present on the pygidium in *T. japonica, T. gigas, T. kerguenlensis 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 ± 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	*T. glandulosa*
	Lateral groove absent	**3**
3	Body grub-shaped, < 25 segments, mid-ventral groove present, very short setae	*T. gravieri*
	Body fusiform, ≥ 25 segments, fascicles of distinguished setae	**4**
4	Segment number 28, ≥ 25 setigers	*T. fusus*
	Segment number 25, 17 setigers	*T. nigrocincta*
5	Prostomium truncated, 31 setigers, large species	*T. foetida*
	Prostomium pointed conical	**6**
6	Branchiae branched	*T. arborifera*
	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	*T. hobsonae*
	Mid-ventral groove and parapodial lappets well developed, 34-35 setigers	*T. fusiformis*
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	*T. gigas*
	Posterior parapodia with small lappets, knob pygidium, length about 3 cm	*T. elongata*
12	Epithelium with large, dorsal and ventral coarse pustules, setiger number to about 45, pygidium with 12-13 irregular papillae	*T. granulata*
	Epithelium finely reticulated, from 44 to 53 setigers, pygidium with 7 cirri	*T. lithophila*
13	Segment number > 30	**14**
	Segment number ≤ 30	**18**
14	Posterior lappets absent, 26-45 setigers	*T. granulata*

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 ..... *T. japonica*
Segment number 35, 33 pairs of branchiae ..... *T. concinna*

17 Segment number 29-32 ..... *T. olens*
Segment number 38-40 ..... *T. olens novae zealandia*

18 Setigers number = 18, 23 segments ..... *T. orogenensis*
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 ..... *T. carnea*
Setigers number ≥ 25 ..... **21**

21 Numbers of branchiae pairs 9-12, 26 setigers and 25-27 segments ..... *T. profundi*
Numbers of branchiae ≥ 15 ..... **22**

22 Segments number 30-32, 25-28 setigers, 22-25 pairs of branchiae number ..... *T. pupa*
Segments number < 30, about 25 setigers, 17-21 pairs of branchiae, anal cylinder surrounded by a circlet of short papillae ..... *T. antarctica*

23 Body pigmented in red purple, 17 pairs of branchiae ..... *T. doellojuradoi*
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 ..... *T. kerguelensis*
Laterals lappets absent, a pair of dorsal anal cirri at the end of the anal cylinder ..... *T. kerguelensis gravieri*

27 Setigers number 23-26, posterior margin of abdominal segment smooth, not scalloped, pygidium ovoid ..... *T. forbesii*
Setigers number 26-29, posterior margin of abdominal ondulate or serrulate, pygidium cylindrical ..... *T. forbesii intermedia*

28 Parapodial lappets little developed, pygidial knob pigmented, 23 setigers, 28 segments ..... *T. horsti*
Parapodial lappets developed, pygidium not pigmented **29**

29 Branchiae number ≥ 20, 27 segments, 24 setigers ..... *T. chiloensis*
Branchiae number ≤ 20, 29 segments **30**

30 Setigers number 23-25 ..... *T. brevis*
Setigers number 27 ..... *T. chinensis*

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. forbesi, T. fusus, T. gravieri, T. japonica, T. kerguelensis, T. olens,* and *T. profundi.*

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

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

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.

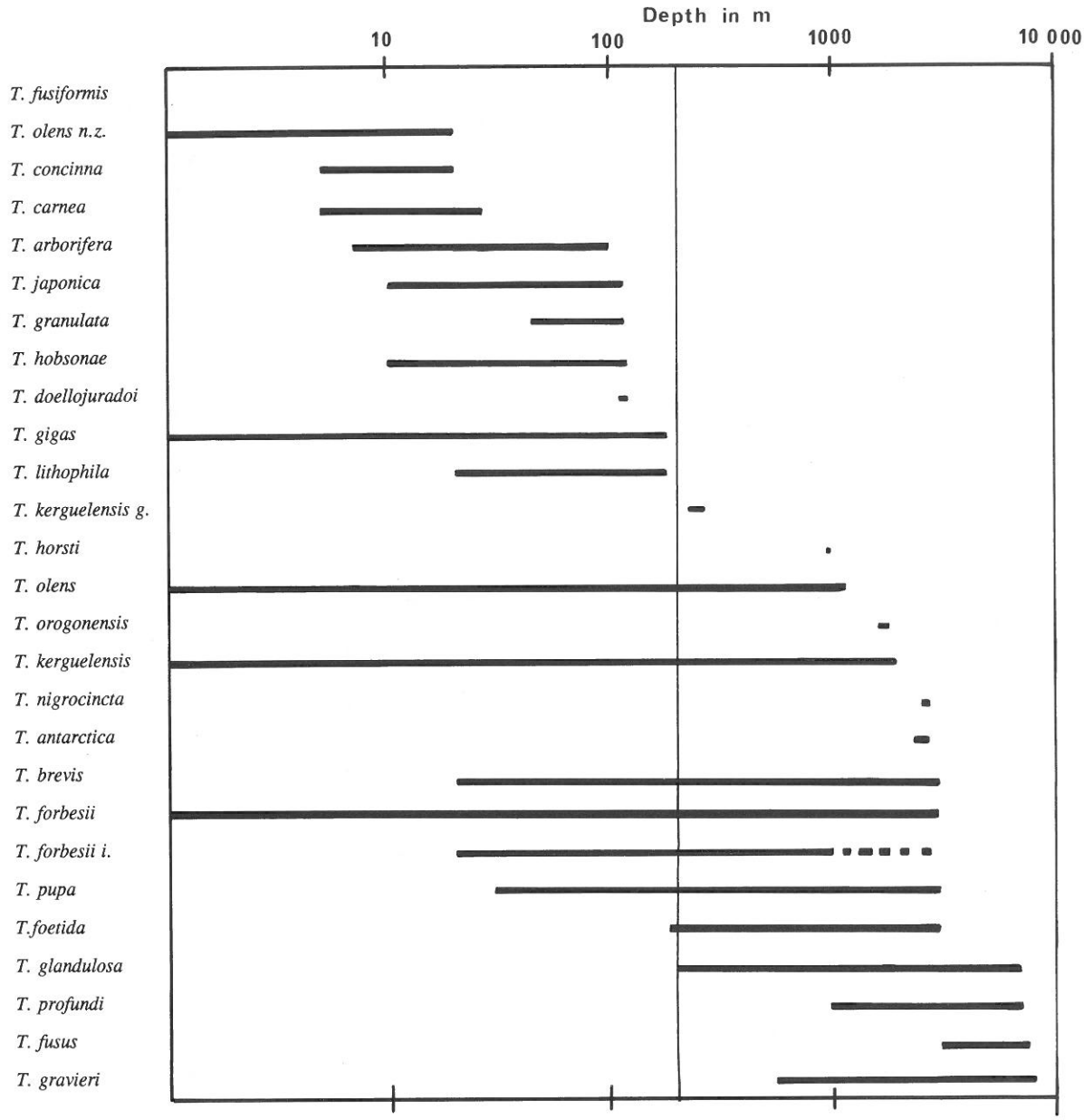

FIG. 1. — Bathymetric distribution of *Travisia* species from the world's oceans.

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 Travisiinae and to the knowledge of the Opheliidae family. The sub-family Travisiinae 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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