

Is *Owenia fusiformis* Delle Chiaje a cosmopolitan species ?

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ABSTRACT

Some works on Polychaetes report that a very large fraction of the class is widely distributed with a large bathymetric range. Nevertheless, several recent studies have shown limited distribution of species or genus in the world; it has also been questioned whether or not any "cosmopolitan" polychaete species exists as a single species. The tube-building polychaete *Owenia fusiformis* is considered to have a world wide distribution with depths ranging from shallow littoral to 4,554 m. However, geographical and bathymetric distribution of this species remains uncertain. The objective of this paper was to bring together all available data in order to present an up-to-date review of the knowledge on the genus *Owenia*. Moreover, some observations of macroscopic morphological characters (the presence of a thoracic collar and eye-spots, the structure of the tube) of specimens collected in Atlantic, Pacific and Indian Oceans were presented. From this study, only two species remain valid: *O. lobopygidiata*, which is a bathyal and abyssal Pacific species, and *O. fusiformis*. *O. collaris* described in the eastern Pacific and Carribean and *O. caudisetosa*, which was only known from the Salvador coasts, are junior synonyms of *O. fusiformis*. Although there is some variability of microscopic and macroscopic morphological characters, these variations do not allow for the identification of several species from *O. fusiformis* populations. *O. fusiformis* seems truly cosmopolitan which is absent only in Antarctic waters. It is a typical sandy and muddy-sandy species. The species is abundant only in shallows waters (0-40 m), but it is found with certainly to 2,325 m. The records from greater depths are doubtful insofar as the specimens are usually fragmented and may be reported as the bathyal species *O. lobopygidiata*. The species is able to develop different reproductive strategies in relation to latitude. Further work is necessary to complete the biological studies of populations especially from the coldest and warmest waters, and to investigate if there are isolated genetic populations.

RÉSUMÉ

Owenia fusiformis Delle Chiaje est-elle une espèce cosmopolite ?

Chez les Polychètes, de nombreux travaux ont mis en évidence une prépondérance d'espèces possédant une large répartition géographique et bathymétrique. Toutefois, des études récentes ont remis en cause ce cosmopolitisme, divisant

les espèces largement distribuées en plusieurs espèces distinctes. L'annélide polychète tubicole *Owenia fusiformis* est une de ces espèces avec une distribution géographique étendue ; elle est présente des eaux littorales aux zones abyssales, jusqu'à 4554 m. Toutefois, cette répartition demeure incertaine. L'objectif de cet article est de présenter une synthèse de l'ensemble des données recueillies sur le genre *Owenia*. De plus, les résultats d'observations de caractères morphologiques macroscopiques (présence d'une collerette thoracique et de taches oculiformes, structure du tube) de spécimens récoltés dans les océans atlantique, pacifique et indien sont présentés. Deux espèces demeurent valides : *O. lobopygidiata*, présente dans les zones pacifiques bathyales et abyssales et *O. fusiformis*. *O. collaris*, décrite dans l'est Pacifique et les Caraïbes et *O. caudisetosa*, décrite et signalée uniquement sur les côtes du Salvador doivent être considérées comme synonymes d'*O. fusiformis*. *O. fusiformis* semble donc être une véritable espèce cosmopolite, absente seulement de l'Océan Antarctique. Caractéristique des sédiments sableux et sablo-vaseux, elle est abondante uniquement dans les eaux côtières (0-40 m) et trouvée avec certitude jusqu'à 2325 m. Les signalisations plus profondes sont douteuses dans la mesure où les spécimens récoltés sont rarement entiers et peuvent se référer à l'espèce abyssale *O. lobopygidiata*. *O. fusiformis* est capable de développer différentes stratégies reproductives en fonction de la latitude. A l'avenir, il est nécessaire de (1) compléter les études de biologie des populations, principalement dans les eaux froides et tropicales et (2) tester si les différentes populations sont génétiquement séparées.

INTRODUCTION

FAUVEL (1959) reported that there are no biogeographical regions for the polychaetes. Available data on the polychaetes confirm that a very large fraction of the class is widely distributed or with a large bathymetric range (HOLTHE, 1978). Nevertheless, several studies show limited distribution of the species or genus in the world wide ocean (WELLS, 1963; KNIGHT-JONES *et al.*, 1991). The tube-building polychaete *Owenia fusiformis* Delle Chiaje is reported to have a world wide distribution from low-water mark to 4,554 m (HARTMAN, 1965). However, the geographical and bathymetric distribution of *O. fusiformis* is uncertain as it is questionable whether any "cosmopolitan" polychaete species is a single species (NILSEN & HOLTHE, 1985). Since the beginning of the century, a large geographical distribution of the species was cited by GRAVIER (1906). The objective of this paper is to bring together all available data in order to present an up-to-date review of bathymetry, ecological and geographical distribution, biology and morphology of *O. fusiformis*. This work is limited by several methodological problems such as: (1) most of the available data came from ecological studies which had not confirmed the species true identity; (2) many authors had just seen the tubes of *Owenia* and automatically referred them to *O. fusiformis* without examining the specimens. Therefore, in a preliminary work, to define the occurrence of one or more species of *Owenia*, some morphological characters of specimens from different localities of the Atlantic, Pacific and Indian oceans were examined.

HISTORICAL

Although the synonymy of different species was not always confirmed by the examination of type specimen, HARTMAN (1959) considered six valid species of *Owenia* in her catalogue:

Owenia artifex (Verrill, 1885). *Ammochares artifex* VERRILL, 1885: 439.

Owenia fusiformis Delle Chiaje, 1841; *Owenia fusiformis* Delle Chiaje, 1841: 31. *Ammochares aedificator* ANDREWS, 1891: 296, pl. 14, figs 42-45. *Ammochares assimilator* CAULLERY, 1944: 49 [error for *A. aedificator* Andrews, 1891]. *Ammochares assimilis* SARS, 1851: 201. MALMGREN, 1867: 210, pl. 12, fig. 65. *Ammochares ottonis* GRUBE, 1846: 164, pl. 5, fig. 2. *Ops digitata* CARRINGTON, 1865: 187. *Owenia assimilis* LEVINSEN, 1883: 148. WOLLEBAEK, 1912: 30, pl. 1, fig. 6. *Owenia brachycera* MARION, 1876: 312. *Owenia filiformis* -CLAPAREDE, 1868: 446, pl. 26, fig. 5. ? *Ammochares brasiliensis* HANSEN, 1882: 19, pl. 5-6, figs 33-36, 1-4. ? *Ammochares occidentalis* (JOHNSON, 1901 : 420, pl. 14, figs 140-142. ? *Ammochares sundevalli* KINBERG, 1867 : 343 ? *Ammochares tegula* KINBERG, 1867: 343.

Owenia collaris Hartman, 1955. *Owenia fusiformis collaris* Hartman, 1955: 46, pl.2, figs 6-7. *Owenia collaris* HARTMAN, 1969: 493.

Owenia lobopygidiata Uschakov, 1950. *Owenia lobopygidiata* Uschakov, 1950: 214, fig. 31. *Owenia lobopygidiata* USCHAKOV, 1955: 347, fig. 128 E-J.

Owenia orientalis (Grube, 1878). *Ammochares orientalis* GRUBE, 1878 : 204, pl. 10, fig. 6.

Owenia tenuis (Haswell, 1883). *Ammochares tenuis* HASWELL, 1883: 633, pl. 12, fig. 2.

Since Hartman's catalogue, only one species *Owenia caudisetosa* Hartmann-Schröder, 1959 has been described from Estero Jaltepeque, Salvador, Pacific. HARTMAN (1969) then raised *O. fusiformis collaris* Hartman, 1955 to specific rank as *O. collaris*, again clearly stating that *O. fusiformis* lacks a collar. FAUVEL (1953) gave *Ammochares orientalis* Grube, 1878 as a synonym of *O. fusiformis*. EHLERS (1901), then RULLIER (1965b) and DAY & HUTCHINGS (1979) considered *O. tenuis* (Haswell, 1883) as *O. fusiformis*. The species *Owenia artifex* (Verrill, 1885) from Cape Cod has not been cited since its description although many studies have been made in this region. This species is doubtful as its description corresponds to *O. fusiformis*; it is probably a synonym of *O. fusiformis*. From this summary, the genus *Owenia* would include four species: *O. caudisetosa*, *O. collaris*, *O. fusiformis* and *O. lobopygiata*.

MORPHOLOGICAL DIFFERENCES BETWEEN SPECIES

The principle morphological characters of *O. fusiformis* are: crown of tentacles projects forward from the head region, tentacular crown divided into two lobes, latero-ventral eye-spots, uncini with two teeth side by side, and pygidium with a pair of weakly developed lobes. DELLE CHIAJE (1841) did not indicate the presence of a collar in Mediterranean specimens. From primary description, the characters distinguishing the other species from *O. fusiformis* are: *O. lobopygiata*, absence of ventral eye-spots and a pygidium with nine finger-shaped papillae; *O. collaris*, presence of a high, thoracic, membranous collar, and uncini with much longer teeth and without a shoulder; *O. caudisetosa*: small size, absence of ventral eye-spot and capillary setae on the first thoracic segment and the presence of one row of dark pigmentation at the branchial base. Three specimens of *O. caudisetosa* were examined. In contrast, with the original description these specimens have three thoracic segments with capillary setae. The presence of a pigmented row at the branchial base and the absence of eyes spots should not be considered as a specific character (see Table 1). All distinctive characters of this species are very similar to those of *O. fusiformis*, and the synonymy of the two species is proposed.

Table 1 gives the principle macroscopic morphological characters observed on specimens from several localities, including individuals from California named as *O. fusiformis collaris* and *O. collaris* by HARTMAN. A thoracic collar is present in all the individuals, but it is more or less developed. Specimens having a thickly developed collar are found on the American Pacific and Atlantic coasts, and Kuwait coast. On the North American coasts, there are specimens with or without a developed collar independent of latitude. On the contrary, on the European and African coasts, all the specimens have a smaller and thinner collar. The eye-spots are absent only in a few cases, but this may be due to preservation. A brown pigment band across a branchial lobes is present in specimens from the Senegal coasts (Table 1). MILLIGAN (1984) reported such brown pigmentation for individuals from the Gulf of Mexico. Different thorax pigmentation (one or two pigmented rows at the branchial base, or general pigmentation) are present principally on subtropical and tropical populations. The tube shows variable granulometric composition and arrangement: grains of quartz and calcareous fragments piled like roof tiles or conglomerated sand grains or sand grains in a fibrous matrix. This tube structure seems to be related to the habitat of the worm. The pygidium does not vary in shape, and all specimens have three setigerous thoracic segments. Worms with a thick developed collar have a shorter branchial crown with the exception of Louisianan specimens which exhibit both short and long branchial crowns. In summary, this study shows that there is more intraspecific variability of some morphological characters than occurrence of several *Owenia* species. Since the thoracic collar occurs in specimens representing records from all parts of the world, the separation between *O. collaris* and *O. fusiformis* seems unjustified. Now, we consider that these two forms should be as *O. fusiformis*.

The number of segments and the number of uncini rows in each torus which were primarily used to distinguish *Owenia* species are correlated with age (THIÉBAUT & DAUVIN, 1992). SEM observations of uncini (THOMASSIN & PICARD, 1972; NIELSEN & HOLTHE, 1985; IMAJIMA & MORITA, 1987; GAMBI, 1989; THIÉBAUT & DAUVIN, 1992) from Mediterranean, Pacific, Atlantic and Indian populations, show a homogeneous shape to this character. THOMASSIN & PICARD (1972) have observed some differences between Mediterranean and Indian specimens; the two teeth arranged side by side do appear to be at the same level for the Indian specimens. In summary, only two species known remain in the genus: *O. fusiformis* and *O. lobopygiata*.

TABLE 1. — Morphological characters (thoracic collar, latero-ventral eye-spots, colouring of the thoracic region and tube structure) of *Owenia* specimens from different localities. N: number of observed specimens; n: number > 10; o : absent; * : present; ** : well developed. * identified as *Owenia collaris*. ** identified as *Owenia caudisetosa*.

| Locality | N | Collar | Eye-spots | Colouring | Tube |
|-----------------------------|---|--------|-----------|--|---|
| Bay of Seine (Fr.) | n | * | * | o | with calcareous fragments |
| N.E. Atl. - 10 m | | | | | piled like roof tiles |
| Bay of Morlaix (Fr.) | n | * | o | o | with shell and calcareous fragments piled like roof tiles |
| N.E. Atl. - 17 m | | | | | |
| Bay of Le Croisic (Fr.) | n | * | * | small pigmented area dorsally | with shell fragments and few sand grains piled like roof tiles |
| N.E. Atl. | | | | | |
| Bay of Prado (Fr.) | n | * | * | o | with shell fragments and few sand grains piled like roof tiles |
| Mediterranean Sea | | | | | |
| Salerno Gulf, Naples (It.) | n | * | * | dark area at the branchial base | with calcareous fragments and sand grains piled like roof tiles |
| Mediterranean Sea, 4-10 m | | | | | |
| North of Adriatic Sea (It.) | 2 | * | * | pigmented row at the branchial base | with conglomerated sand grains |
| Mediterranean Sea | | | | | |
| Po River Delta (It.) | n | * | * | o | - |
| Mediterranean Sea -5 m | | | | | |
| Bay of Alger (Alg.) | n | * | * | small pigmented area dorsally | with calcareous fragments piled like roof tiles |
| Mediterranean Sea | | | | | |
| Senegal coasts | 2 | * | o | pigmented row in the branchial crown and a complete pigmented thorax | with calcareous fragments piled like roof tiles |
| Tropical Atlantic | | | | | |
| Guinea coasts | 1 | * | * | a complete pigmented thorax | with calcareous fragments piled like roof tiles |
| Tropical Atlantic | | | | | |
| Ivory coasts | 1 | * | * | a complete pigmented thorax | with calcareous fragments irregularly arranged |
| Tropical Atlantic | | | | | |
| Benin coasts | 2 | * | * | a complete pigmented thorax | with calcareous spicules |
| Tropical Atlantic | | | | | |
| Newport (U.S.A.) | 2 | ** | o | o | with conglomerated sand grains |
| | | | | | |
| N.W. Atl. - 34 m | | | | | |
| Eastport (U.S.A.) | 1 | * | o | o | - |
| N.W. Atl. | | | | | |
| North Carolina (U.S.A.) | 3 | ** | * | o | - |
| N.W. Atl. - 29 m | | | | | |
| Indian River (U.S.A.) | 2 | * | o | o | with conglomerated sand grains and few calcareous fragments |
| N.W. Atl. | | | | | |
| Louisiane coasts (U.S.A.) | 6 | ** | o | o | with conglomerated sand grains and piled calcareous fragments |
| N.W. Atl. -19.8 m | | | | | |
| Panama coasts * | 1 | ** | * | two pigmented rows at the branchial base | with calcareous fragments piled like roof tiles |
| Trop. Atl. | | | | | |
| Brazilian coasts | 7 | * | * | variable coloration of branchial crown and thoracic region | with calcareous fragments |
| S.W. Atl. - 12 to - 63 m | | | | | |
| Alaska (U.S.A.) * | 2 | ** | * | o | with sand grains and calcareous fragments piled like roof tiles |
| N.E. Pac. | | | | | |
| False Bay (U.S.A.) | 3 | * | * | o | with sand grains piled like roof tiles |
| N. E. Pac. | | | | | |
| San Juan Islands (U.S.A.) | 2 | * | * | brown area on the thoracic region | with conglomerated sand grains |
| N. E. Pac. | | | | | |
| Puget Sound (U.S.A.) | 1 | * | o | o | - |
| N. E. Pac. -23 m | | | | | |
| Off California (U.S.A.) * | 6 | ** | * | o | with conglomerated sand grains |
| N. E. Pac. - 93 m | | | | | |

| Locality | N | Collar | Eye-spots | Colouring | Tube |
|--|---|--------|-----------|---|---|
| Monterey Bay (U.S.A.) N.E. Pac. - 18 m | 1 | * | * | o | - |
| Tomales Bay (U.S.A.) * N.E. Pac. | n | ** | o | o | with sand grains piled like roof tiles |
| Santa Rosa Isl. (U.S.A.) * N.E. Pac. - 15 m | n | ** | * | o | with calcareous fragments piled like roof tiles |
| Santa Catalina I. (U.S.A.) * N.E. Pac. - 33 m | n | ** | * | o | with calcareous fragments piled like roof tiles |
| Salvador coasts ** N.E. Pac. | 3 | * | o | pigmented row in the branchial crown | - |
| Peruvian coasts S.E. Pac. - 34 m | n | * | * | pigmented points in the branchial crown and a pigmented row at the branchial base | with some sand grains in a fibrous matrix |
| Off Kuwait N.W. Ind. | 1 | ** | * | o | with calcareous fragments piled like roof tiles |
| Jervis Bay (Austr.) S.W. Pac. | 8 | * | * | complete pigmented thorax | with calcareous fragments and sand grains piled like roof tiles |
| Hawkesbury (Austr.) S.W. Pac. | n | * | * | complete pigmented thorax | with conglomerated sand grains |

ECOLOGICAL AND BIOLOGICAL CHARACTERISTICS

O. fusiformis is a typical soft-bottom species. It is found in a large granulometric spectrum from mud to coarse sand but it usually inhabits muddy sand/sandy sediments. In the English Channel, *O. fusiformis* is present only in bays and estuaries where fine sediments are confined in relation to low tidal currents (CABIOCH, pers. comm.). On the contrary, in the North Sea, *O. fusiformis* is widely distributed according widespread occurrence of fine sediment (DEWARUMEZ, pers. comm.). On the Texas continental shelf, it is found in sandy sediment with a relatively low mud content (FLINT & RABALAIS, 1980).

O. fusiformis can feed in an upright position or bent over towards the substratum; thus it can be either a filter-feeder or surface deposit-feeder (FLINT & RABALAIS, 1980; GAMBÌ, 1989). It forms a crater around its tube, and it plays an important role in surface bioturbation (GAMBÌ, 1989). It is reported as a common prey for some flat fishes in the area where the population is dominant (EMMETT *et al.*, 1987; MÉNARD *et al.*, 1989).

The species can live three or four years in the English Channel. It is a polythelic polychaete, and only some specimens can reproduce at one year (MÉNARD *et al.*, 1989; GENTIL *et al.*, 1990). The effective fecundity is correlated with the length of the female which varies from 6,000 oocytes for a female of 40 mm in length to 85,000 oocytes for a female of 110 mm in length (THIÉBAUT & DAUVIN, 1991).

Owenia is known to produce a distinctive planktotrophic larvae (WILSON, 1932). In the Bay of Seine, English Channel, GENTIL *et al.* (1990) reported an annual reproductive cycle with a short summer sexual pause, a gonadal development during the autumn and spawning occurring from May to June. Recruitment occurred at the end of spring (DAUVIN, 1992). WILSON (1932) also reported mature adults from March to July with spawning in June in the Plymouth area. BHAUD (1972) compared his planktonic data from subtropical conditions (western Mediterranean) with results from boreal waters (southern Scandinavia). He showed a shorter occurrence of the mitraria larvae in northern waters (mid-June to mid-August) compared with southern waters (February to the end of June). CAZAUX (1973) reported the presence of larvae in planktonic samples from February to April in the Arcachon Bay. BUCHANAN *et al.* (1978) observed a marked summer recruitment in a population from the South Northumberland coasts, North Sea. These observations with an annual reproductive cycle are obviously different from those of Mc NULTY & LOPEZ (1969) who described a year-round breeding population in the subtropical waters of Biscayne Bay, Florida, but the life span is shorter in these warm waters. FAGER (1964) for a Californian population, which lives at least two years, observed a main spring recruitment, but also some new recruits through the year. In Disko Bay, West Greenland, *O. fusiformis* reproduced asexually by fragmentation and regeneration in the absence of favourable conditions for gametogenesis and spawning (CURTIS, 1977).

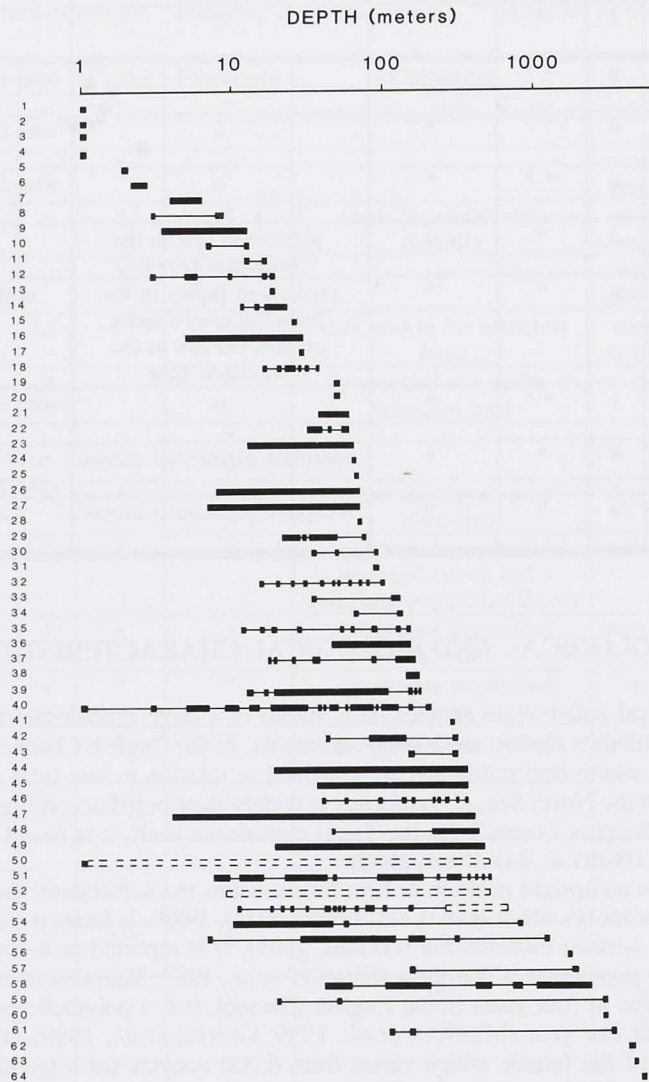


FIG. 1. — The bathymetric distribution of *O. fusiformis*. The thick line indicates effective depths of sampling, and the thin line the possible area of bathymetries. From: 1: AMOUREUX (1966), 2: ANDREWS (1891), 3: de SAINT JOSEPH (1898), 4: VOVELLE (1963), 5: JELDES & LEFEVERE (1959), 6: NICOLAIDOU *et al.* (1988), 7: CAPACCIONI *et al.* (1991), 8: NICOLAIDOU & PAPADOPOULOU (1989), 9: COGNETTI-VARRIALE & ZUNARELLI-VANDINI (1979), 10: COGNETTI-VARRIALE & ZUNARELLI-VANDINI (1978), 11: GIANGRANDE & GAMBI (1986), 12: GIBBS (1971), 13: GEORGE (1974), 14: CHARDY *et al.* (1987), 15: FAUVEL & RULLIER (1959a), 16: WOLFF (1973), 17: GILLET (1985), 18: ELIASON (1962), 19: RULLIER (1965a), 20: HARTMANN-SCHRÖDER & HARTMANN (1965), 21: HARTMANN (1944b), 22: CLAVIER & GARRIGUE (1990), 23: RULLIER & AMOUREUX (1979), 24: BERKELEY & BERKELEY (1952), 25: IMAJIMA (1961), 26: WILLEY (1902), 27: BRUCE *et al.* (1963), 28: DUMITRESCO (1960), 29: MICHAELSEN (1897), 30: FOURNIER & LEVINGS (1982), 31: FAUVEL (1909), 32: INTÈS & LE LOEUFF (1977), 33: BELLAN (1969b), 34: IMAJIMA (1963), 35: DAY (1961), 36: MILLIGAN (1984), 37: THÉEL (1879), 38: AMOUREUX (1973), 39: WESENBERG-LUND (1951), 40: IMAJIMA & MORITA (1987), 41: FAUVEL (1911), 42: BIDENKAP (1907), 43: AMOUREUX (1972), 44: BIDENKAP (1894), 45: DANIELSSEN (1859), 46: HARTMANN-SCHRÖDER (1974a), 47: WOLLEBAEK (1912), 48: HARTMANN-SCHRÖDER (1986), 49: EHLERS (1875), 50: DAY (1967), 51: WESENBERG-LUND (1950b), 52: USCHAKOV (1955), 53: KIRKEGAARD (1959), 54: CAULLERY (1944), 55: McINTOSH (1915), 56: KIRKEGAARD (1983), 57: WESENBERG-LUND (1950a), 58: BILYARD & CAREY (1979), 59: FAUVEL (1932), 60: HARTMAN (1966), 61: McINTOSH (1879), 62: KIRKEGAARD (1980), 63: HARTMAN (1965), 64: ELIASON (1951).

TABLE 2. — Records of *Owenia* species at depths below 500 m. Condition of sampled individuals is given.

| DEPTHS (m) and SITES | AUTHOR | SAMPLE CONDITIONS |
|--|------------------------|--|
| 500-1,366; Okhotsk Sea | USHAKOV (1955) | <i>O. lobopygidiata</i> |
| 775-3,225; Beaufort Sea | BILYARD & CAREY (1979) | no information |
| 798; Molucca Sea | CAULLERY (1944) | one worm named <i>O. fusiformis</i> but posterior part absent without pigmentation and no ventral eyespots: may be <i>O. lobopygidiata</i> |
| 1,152; N.E. Atlantic | McINTOSH (1915) | no information |
| 1,620-1,700; N.E. Atlantic | KIRKEGAARD (1983) | two specimens |
| 1,800; N.E. Atlantic | WESENBERG-LUND (1950a) | 10 worms in tubes with few foraminiferan tests |
| 2,700; N.E. Indian | FAUVEL (1932) | only tubes with few foraminiferan tests |
| 2,725; Antarctic | HARTMAN (1966) | tube fragment only, as ? <i>Owenia</i> sp. |
| 3,213; N.W. Atlantic | McINTOSH (1879) | as <i>O. fusiformis</i> , only one tube fragment with foraminiferan tests |
| 4,120; N.E. Atlantic | KIRKEGAARD (1980) | one fragmentary worm as <i>O. ?fusiformis</i> |
| 4,250; N.E. Atlantic | KIRKEGAARD (1980) | five empty tubes as <i>O. ?fusiformis</i> |
| 4,554; N.W. Atlantic | HARTMAN (1965) | tubes covered with foraminiferan tests of <i>O. ?fusiformis</i> |
| 5,033-5,044; N.W. Atlantic | ELIASON (1951) | <i>Owenia</i> ? sp., fragments of tubes covered with foraminiferan test, with remnants of worm |
| 6,490-6,650; Banda Trench Indo-Pacific | KIRKEGAARD (1956) | ? <i>O. lobopygidiata</i> ; fragments and tubes |
| 6,580; Banda Trench Indo-Pacific | KIRKEGAARD (1956) | ? <i>O. lobopygidiata</i> ; one specimen and fragments |

BATHYMETRIC DISTRIBUTION OF *OWENIA* SPECIES

O. fusiformis is found on the continental shelf 0-200 m (Fig. 1) with only 10 records exceeding 500 m and six 2,500 m. Few specimens are found depths greater than 500 m, and usually the animal is incomplete or only tube fragments are found. Most of reports citing *O. fusiformis* from below 500 m (Table 2) are not precise for the *O. fusiformis* status. These include: 1) tubes or tube fragments without worms but with foraminiferan tests proving the bathyal or abyssal origin; 2) identification with doubt as *O. ?fusiformis* or *Owenia* ? sp. or ? *Owenia* sp.; and 3) incomplete worms that do not permit a specific identification. It is probable that many of the *Owenia* specimens found in deep water are *O. lobopygidiata*. The maximum depth of *O. fusiformis* appears to be 2,325 m in the Beaufort Sea (BILYARD & CAREY, 1979).

O. lobopygidiata is a western Pacific species present in Okhotsk Sea and Bering Sea from 110 to 1366 m (USCHAKOV, 1955) and with doubts in the abyssal Banda Trench at 6,490-6,650 m (KIRKEGAARD, 1956).

BIOGEOGRAPHICAL DISTRIBUTION OF *OWENIA FUSIFORMIS*

Owenia fusiformis occurs both sides of the Atlantic Ocean except along the north Brazilian coasts where the observations of polychaetes are limited (Fig. 2). In the eastern Atlantic, it has been observed from the north of Norway to South Africa. It is absent from the Baltic Sea. In the Mediterranean waters, it presents principally in the western part. It has been reported from the Bosphore in the Black Sea. In the western Atlantic, it is present from the Gulf of St Lawrence to Rio de la Plata, Argentina. In the Arctic, it is reported along both coasts of southern Greenland at 75°N latitude. It reaches 80°N latitude, at Spitzberg Island and the New Zemble Island. It is also reported in the Kara Sea and the Beaufort Sea (Figs 2-3).



FIG. 2. — The atlantic distribution of *O. fusiformis*. From AMOUREUX (1966, 1970, 1971, 1972, 1973, 1976), ANADON (1980), ANDREWS (1891), AUGENER (1928), BACHELET (1981), BAKALEM & ROMANO (1978), BAKALEM (pers. comm.), BELLAN (1969a,b), BIDENKAP (1894, 1907), BRUCE *et al.* (1963), BUCHANAN (1957), BUCHANAN *et al.* (1978), CAPACCIONI -AZZATI *et al.* (1991), CASTELLI *et al.* (1991), CLAPARÈDE (1868), COGNETTI-VARRIALE & ZUNARELLI-VANDINI (1979), CURTIS (1972, 1977), DALE *et al.* (1989), DANIELSSEN (1859), DAY (1961, 1967), DAY *et al.* (1971), DEWARUMEZ (pers. comm.), DIAPOULIS & BOGDANOS (1983), DUMITRESCO (1960), EAGLE (1973), EAGLE & HARDIMAN (1976), EHLERS (1875), ELIASON (1962), FAUVEL (1909, 1911, 1936, 1937), FAUVEL & RULLIER (1959a,b), FRANKENBERG & LEIPER (1977), GAGE (1972), GAMBI & GANGRANDE (1986), GEORGE (1974), GIANGRANDE & GAMBI (1986), GILLET (1985, 1988), GLÉMAREC (1969), GUELORGET & MICHEL (1979), GUILLAUMONT & HAMON (1983), HAMOND (1966), HARTMAN (1944), HARTMANN-SCHRÖDER (1971, 1974b), HASSAM (1991), HOLTHE (1977b), IBANEZ AGUIRRE & SOLIS WEISS (1986), INTES & LE LOEUFF (1977), JELDES & LEFEVERE (1959), JOHNSON (1901), KINBERG (1867), KIRKEGAARD (1959, 1969, 1978, 1983), LABORDA (1987), LAUBIER (1962), LAVERDE-CASTILLO & GOMEZ (1987), LOPEZ-JAMAR (1981), LOPEZ-JAMAR *et al.* (1986), LUNA (1967), MCCALL (1977), MCINTOSH (1879, 1915), MCINTYRE (1958), McNULTY & LOPEZ (1969), MALMGREN (1867), MARINOV (1977), MASSÉ (1971), MICHAELSEN (1897, 1898), MILLIGAN (1984), NICOLAIDOU *et al.* (1988), NICOLAIDOU & PAPADOPOULOU (1989), NILSEN & HOLTHE (1985), NONATO & LUNA (1970), ORENSANZ & GIANUCA (1974), PEER *et al.* (1980), PROBERT (1981), QUINTINO & GENTIL (1987), REES (1983), REES *et al.* (1976), RIOJA (1917), RULLIER (1963, 1965a), RULLIER & AMOUREUX (1979), SANZ (1986), SHIN *et al.* (1982), STEIMLE (1982), TORRES-GAVILA *et al.* (1990), TREADWELL (1948), TUNBERG (1982), VOVELLE (1963), WACASEY *et al.* (1979), WESENBERG-LUND (1950a, b, 1951, 1953), ZGHAL & BEN AMOR, (1980), ZUNARELLI-VANDINI & COGNETTI-VARRIALE (1981).

In the eastern part of the Pacific Ocean (Fig. 3), it is recorded from Alaska to south California and along the Peruvian and Chilean coasts where it was named *O. fusiformis* or *O. collaris*. In the western part, it is reported from the Bering Sea to Tasmania and New Zealand. It has not been reported from the mid central ocean islands. In the Indian Ocean (Fig. 3), it is present in Bengal Gulf, Arabic Gulf, Mozambic Channel and along Madagascar coasts. It is unknown from the Arabic peninsula to the Mozambique coasts.

In summary, *O. fusiformis* is present along most of the coasts of the Atlantic and Pacific Oceans, it appears less extended in the Indian Ocean and absent in the Antarctic Ocean. Several authors reported *O. fusiformis* as present in this southern Ocean, but the single reference (HARTMAN, 1966) is doubtful because the fragments of tubes were named as ? *Owenia* sp. (Table 2). Therefore, the species occurs in tropical, temperate and arctic areas.

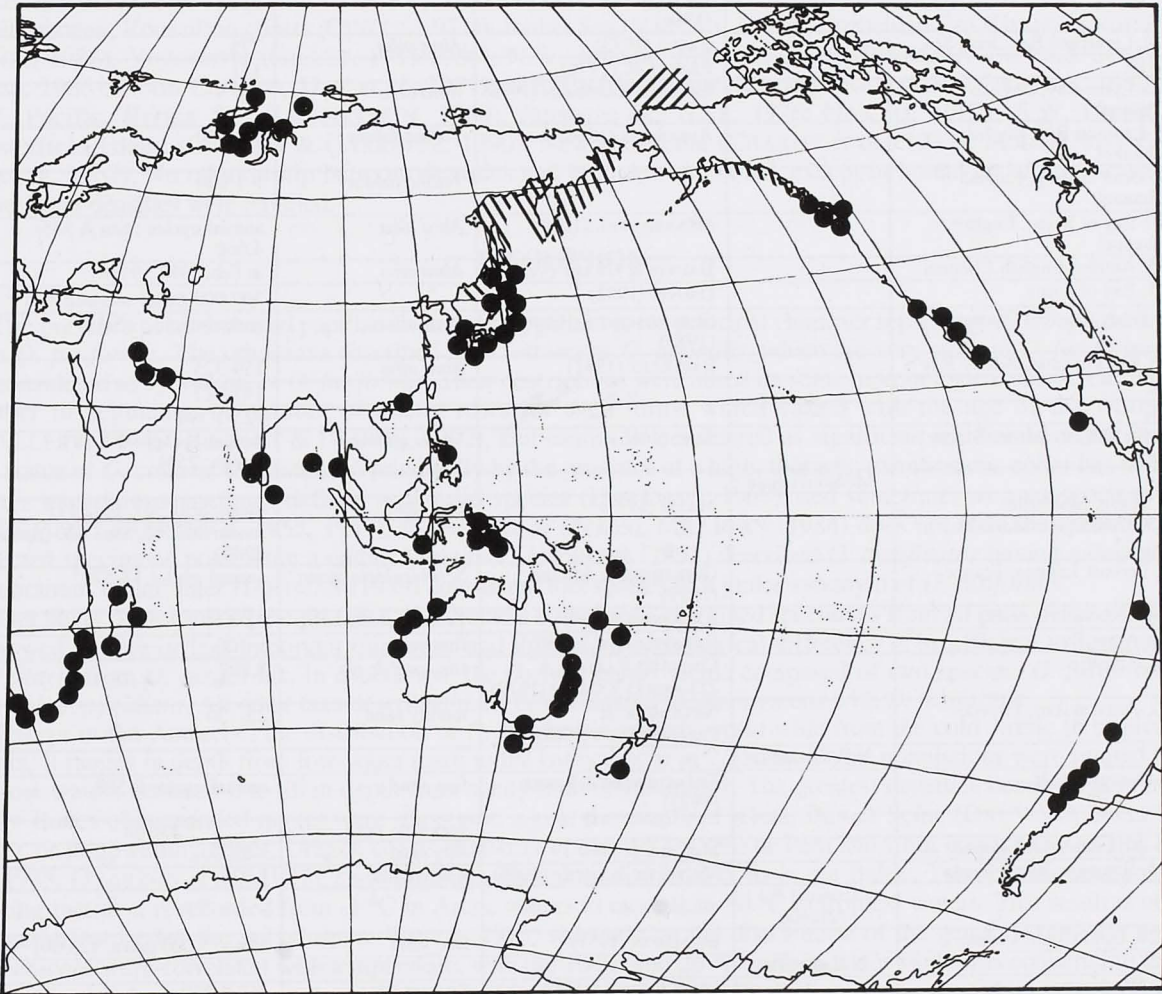


FIG. 3. — The indo-pacific distribution of *O. fusiformis*. From BERKELEY & BERKELEY (1952), BILYARD & CAREY (1979), CAULLERY (1944), CHARDY *et al.* (1987), CLAVIER & GARRIGUE (1990), DAY (1961, 1967), DAY & HUTCHINGS (1979), EHLERS (1901), FAGER (1964), FAUVEL (1911, 1919, 1921, 1932), FOURNIER & LEVINGS (1982), GIBBS (1971), GRUBE (1878), HARTMANN-SCHRÖDER & HARTMANN (1965), HARTMANN-SCHRÖDER (1979, 1980, 1981, 1989, 1990), HASWELL (1883), HOBSON & BANSE (1981), HUTCHINGS (1973), HUTCHINGS & RAINER (1979), IMAJIMA (1961, 1963), IMAJIMA & MORITA (1987), LEE (1976), LEVENSTEIN (1960), LIE & KISKER (1970), NAKO (1982), OKUDA (1937), PLANTE (1967), RAINER (1981), ROZBACZYLO (1985), RULLIER (1965b), SARTI MARTINEZ & SOLIS-WEISS (1987), SHIN & THOMPSON (1982), STEPHENSON & CAMPBELL (1977), TAMPI & RANGARAJAN (1964), THEEL (1879), USCHAKOV (1955), WESENBERG-LUND (1949), WILLEY (1902), WIREN (1883).

TABLE 3. — Records of the main populations of *Owenia fusiformis* (maximal density higher than 100 ind. m⁻² or average density higher than 50 ind. m⁻²). Site, depth and type of community are precised (sieving on 1 mm mesh, except 1: 0,280 and 2: 0,5 mm).

| DEPTHS (m) and SITES | | AUTHOR | TYPE OF COMMUNITY | DENSITY (ind.m ⁻²) |
|--|----------------------|---|---------------------------------|--|
| | N.E. Atlantic | | | |
| 20-150, Scottish Sea lochs | | GAGE (1972) | muddy sand | two stations : 140, 180 |
| 30, Dogger bank, North Sea | | KIRKEGAARD (1978) | <i>Venus gallina</i> | mean : 74 |
| 30, German Bight, North Sea | | RACHOR (1978) | <i>Nucula turgida</i> | annual cycles: 0-188 |
| 30, German Bight, North Sea | | SALZWEDEL <i>et al.</i> (1985) | " | 0-135 |
| 20-40, " " | | HICKEL <i>et al.</i> (1989) | <i>Abra alba</i> | several stations: 0-203 |
| 15, N.E. England, North Sea | | REES (1983) | <i>Venus gallina</i> | 160 |
| 55, Nothumberland, North Sea | | BUCHANAN <i>et al.</i> (1978) BUCHANAN & MOORE (1986) | <i>Amphiura fififormis</i> " | annual cycle: 50-410 mean 74/80: 75 ; 81/85: 63 |
| 10, Liverpool Bay, Irish Sea | | EAGLE (1973) | <i>Abra alba</i> | 275 |
| 2-10, " " | | REES <i>et al.</i> (1976) | " | 111 |
| 40, Lyme Bay, English Channel | | EAGLE & HARDIMAN (1976) | <i>Abra alba</i> | 127 |
| 0, Lannion Bay, English Channel | | AMOUREUX (1966) | <i>Tellina fabula</i> | > 1,000 |
| 0, Orne estuary, English Channel | | " | <i>Tellina fabula</i> | > 1,000 |
| 10, Bay of Seine, English Channel | | MÉNARD <i>et al.</i> (1989) | <i>Abra alba</i> | annual cycles : Stn A 385-4,660 |
| 35, Antifer, English Channel | | DAUVIN & GILLET (1991) | <i>Abra alba</i> | in Feb. 1987 : 9136 |
| 25, Bay of Seine | | DAUVIN (1992) | " | 300,000 (after recruitment) ¹ |
| 5, Penly, English Channel | | GUILLAUMONT & HAMON (1983) | <i>Abra alba</i> | annual cycle : 15-117 |
| 23, Off Gironde, Biscay Bay | | BACHELET (1981) | <i>Abra alba</i> | 159-325 |
| 30, " " | | " | " | 147-422 |
| 38, " " | | " | " | 125-1,394 |
| 5-40, Off Arcachon, Biscay Bay | | SANZ (1986) | <i>Venus gallina</i> | annual cycles : 0-2,147 (mean: 254) |
| | Mediterranean | | | |
| 5, Prado, Marseille | | MASSÉ (1971) | fine sand | mean: Stn1 367, Stn2 177 |
| 6-7, Camargue, Marseille | | " | " | mean: Stn2 82, Stn3 620 (max. 4940) |
| 1, Prevost Laguna, France | | GUELORGET & MICHEL (1979) | <i>Scrobicularia plana</i> | annual cycle: 13-570 |
| 7-10, Roussillon coasts | | AMOUREUX (1974) | <i>Tellina fabula-tenuis</i> | 72-444 |
| 10, Alger Bay | | BAKALEM <i>et al.</i> (1989) | fine sand | > 100 |
| 12, Adriatic | | COGNETTI-VARIALE & ZUNARELLI-VANDINI (1979) | fine sand & silt | 8,892 |
| 10, Amvrakikos, Greece | | NICOLAIDOU & PAPADOPOULOU (1989) | muddy sand | 25-130 |
| | N.W. Atlantic | | | |
| 9, Georgia shelf | | FRANKENBERG & LEIPER (1977) | fine sand | annual cycle: 0-508 |
| 8, " " | | " | very fine sand | " : 20-108 |
| 15-20, Long Island Sound | | McCALL (1977) | silty sand | > 2,000 |
| 3-5, Biscayne Bay, Florida | | McNULTY & LOPEZ (1969) | sandy mud | 1,926 |
| | Tropical E. Atlantic | | | |
| 5-20, Gold Coast, Guinea | | BUCHANAN (1957) | fine sand | mean: 5,000 (max. 12,000) |
| | N.E. Pacific | | | |
| 36, Washington coasts | | LIE & KISKER (1970) | fine sand & silt | 460-2,300 |
| littoral, Oregon coasts | | EMMETT <i>et al.</i> (1987) | fine sand | mean Sept.: 12,352 (max. 50,246) ² |
| littoral, Oregon coasts | | EMMETT <i>et al.</i> (1988) | fine sand | mean Jul.: 61,582 |
| 8-12, La Jolla Bay, Calif. | S. W. Pacific | FAGER (1964) | fine sand & silt | mean: 500-1,000 (max. 15,000) ² |
| | S.E. Pacific | | | |
| littoral, Blueskin Bay, N.Z.As <i>O. collaris</i> | | RAINER (1981) | shell sand | mean: 4,045 (max. 7,500) |
| 15, Peruvian coasts | | TARAZONA <i>et al.</i> (1985, 1988) | fine sand | max.: 18,950 |
| 10, Concepcion Bay, Chili | | OYARZUN <i>et al.</i> (1987) | very fine sand | about 5,000 |

POPULATION DISTRIBUTION OF OWENIA FUSIFORMIS

Maximal density (> 100 ind. m^{-2}) or mean density (> 50 ind. m^{-2}) found in the literature are shown in the Table 3. Maximal densities are found in shallow waters (0-40 m) from fine sand to muddy sand in *Venus*, *Tellina* or *Abra alba* communities (Table 2). On 0.5 mm sieve mesh, the densities reach a maximum of 300,000 juveniles. m^{-2} during July in the Bay of Seine, English Channel (DAUVIN, 1992), and 50,000 ind. m^{-2} during September on the Oregon coast (EMMET *et al.*, 1987, 1988). Densities about 5,000 ind. m^{-2} are also reported from the French Mediterranean (MASSÉ, 1971), the Gold coast, Guinea, California, Peru, Chili, and New Zealand (Table 2).

The greater densities were found in cold-temperate waters rather than tropical waters. The other quantitative data with lower densities were: N.E. Atlantic, Norway (HOLTJE, 1977a), North Sea (Mc INTYRE, 1958), Spanish coasts (ANADON, 1980; LOPEZ JAMAR, 1981; LOPEZ JAMAR *et al.*, 1986), Morocco (GILLET, 1988); Mediterranean, Roussillon coasts (GUILLE, 1971), Ionian Sea (VATOVA, 1975), Tyrrhenian Sea (GIANGRANDE & GAMBI, 1986), Yugoslavia (GILLET, 1985/1986); N.W. Atlantic, Mexican coasts (IBANEZ AGUIRRE & SOLIS-WEISS, 1986), North Carolina (DAY *et al.*, 1971); N.E. Pacific, Columbia coast (FOURNIER & LEVINGS, 1982); N.W. Pacific, Bering Sea (LEVENSTEIN, 1960), Japanese Sea (LEE, 1976; NAKAO, 1982); S.W. Pacific, Chesterfield Island (CLAVIER & GARRIGUE, 1990), New Caledonia (CHARDY *et al.*, 1987); Indian, Nosy Bé (PLANTE, 1967). No relationship between densities and latitude were noted, except in boreal and Arctic waters where lower densities were reported.

DISCUSSION

The presence of nine shaped papillae around the pygidium is the principal character separating *O. lobopygidiata* from *O. fusiformis*. The other taxa described as *O. ottonis* or *O. assimilis*, which are very close to *O. fusiformis*, are considered as synonyms of *O. fusiformis*. Their descriptions were based on some morphological characters: e.g. number of segments, or number of uncini rows for each torus, which varied with the age of the worms (CAULLERY, 1944; THIEBAUT & DAUVIN, 1992), and cannot be considered as significant taxonomic characters. The status of *O. collaris* characterised principally by the presence of a high, thoracic, membranous collar has been always uncertain, sometimes defined as a valid species (HARTMAN, 1969), and sometimes as a subspecies of *O. fusiformis* (HARTMAN, 1955, 1959). In the Gulf of Mexico, MILLIGAN (1984) does not state the identity of collected specimens possessing a collar. Moreover, ANDREWS (1891) described *O. aedificator* having a delicate membranous collar; later HARTMAN (1959) considered this species as a junior synonym of *O. fusiformis*.

Our study demonstrated the presence of a thoracic collar in all examined specimens from all parts of the world. It showed a more or less important thickness, and this sole morphological difference is insufficient to separate: *O. collaris* from *O. fusiformis*. In conclusion, the *Owenia* genus seems composed of two species: *O. fusiformis* and *O. lobopygidiata*. All other taxa described must be considered as synonymous with *O. fusiformis*.

Except in the Antarctic, the distribution of *O. fusiformis* extends world wide from the cold Arctic to tropical waters. It ranges in depth from low-water mark to the bathyal zone at 2,350 m. Dense populations were limited to shallow waters between 0 to 40 m depth from sandy-mud communities. The greatest densities occurred in areas where fluxes of suspended matter were important: e.g. at the mouth of rivers, Bay of Seine (DAUVIN & GILLET, 1991), or in upwelling zones, Oregon coasts (EMMETT *et al.*, 1987, 1988) or Peru and Chili coasts (TARAZONA *et al.*, 1985; OYARZUN *et al.*, 1987). Low salinities limited its distribution, as in the Baltic. Temperature was not a limiting factor; it is recorded from -1 °C in Arctic waters to more than 30 °C in tropical waters. This result is not a general feature for the polychaetes. WELLS (1963) showed that the distribution of the genera *Arenicola* and *Abarenicola* were correlated with temperature, with the 10 °C and 20 °C surface-water isotherms constituting the most effective barriers for species distribution. Nevertheless, a latitudinal cline of the reproductive period is observed from cold to tropical waters. *O. fusiformis* shows an absence of sexual reproduction in Disko Bay where the species is at its northern limit of distribution forming probably a pseudo-population (CURTIS, 1977).

In the English Channel and North Sea, the species shows a spring and summer spawning and recruitment. In the "Golfe du Lion" and Arcachon Bay a winter spawning and recruitment occurred when the sea bottom temperatures were above 12 °C. Recruitment occurred throughout the year in Florida (Key Biscayne) where the water temperature ranged between 23 °C and 28 °C (Mc NULTY & LOPEZ, 1969). This showed that *O. fusiformis* adapts its reproductive strategy to a very broad temperature scale.

The rate of endemism described in some regions (HARTMAN, 1955) should become less as soon as the distribution of some of the species is better known (KIRKEGAARD, 1969). The Polychaeta are generally ancient and

seem to be very conservative (HOLTHE, 1978), which should explain the wide geographical distribution of some species (FAUCHALD, 1984). Cosmopolitan distribution is known for several species of Polychaeta. Nevertheless, three cases of cosmopolitanism can be defined: 1) true cosmopolitan distribution: the distribution of a species is really world wide as is *O. fusiformis*; 2) the species is distributed world wide but sibling species have been demonstrated: e.g. *Capitella capitata* (GRASSLE & GRASSLE, 1976); or 3) several species have been confused under the same name: e.g. *Terebellides stroemi* which was divided into five species after a morphological study of specimens from several geographical areas (WILLIAMS, 1984) or *Spio filicornis* which was used for several species of *Spio* (DAUVIN, 1989). Finally, the number of cosmopolitan species could be overestimated (BHAUD, 1982). This is due to three principal causes: 1) the absence of adequate identificatory keys for many parts of the world, 2) the frequent identification of polychaetes by benthic ecologists doing identification work strictly from need, and 3) the poor description of many species (FAUCHALD, 1984).

Recent taxonomic studies of Australian material have revealed in many cases that the species previously identified as the cosmopolitan species *Lanice conchilega* (Pallas, 1766) and *Eupolymnia nebulosa* (Montagu, 1818) were in fact new species (HUTCHINGS & GLASBY, 1988). Moreover Australia is known to have a high speciation rate.

No relationship between the type of development and the range of the distribution of a species has been noted (BHAUD, 1982, 1984). Larval stages of certain species could play a role in dispersion (BHAUD, 1982). The main explanation for a wide distribution seems to be the specific responses to physico-chemical, especially temperature conditions (BHAUD, 1982; GOLIKOV *et al.*, 1990). Within the entire distributional area of a species there exists a distinct interrelation between the genetically determined requirements of its individuals and the environment. The distributional pattern indicates a certain unity between the species and its environment, and GOLIKOV *et al.* (1990) suggested the term "ecogenocomplex" for this kind of relationship.

From the data set collected in this work, *O. fusiformis* seems to be a true cosmopolitan species. Since its description by DELLE CHIAJE (1841), several authors have described different species of *Owenia* or, suggested the existence of races of *O. fusiformis* (CAULLERY, 1944; THOMASSIN & PICARD, 1972) by some morphological characters such as the presence of a thoracic collar, the number of segments, the shape of uncini, the length of thoracic setae. However, the morphological and physiological characters used seem to be the result of an interindividual variability and do not permit to separation without ambiguity distinct species. Therefore, most of *Owenia* species described since DELLE CHIAJE have later been considered as a junior synonym of *O. fusiformis*. It is clear that now, as in the past, the macroscopic and microscopic observations or comparisons of morphological characters alone are insufficient to distinguish some possible distinct species of *O. fusiformis*.

In the future, it should be necessary to study *Owenia* with biological and molecular points of view to define its status. Studies must be developed on: 1) the variability and adaptations of reproductive strategy in relation to latitude including extreme conditions as the Arctic and tropical seas; 2) enzymatic and mtDNA polymorphism. For example, GRASSLE & GRASSLE (1976) showed that sibling *Capitella* species with slight morphological differences, and close life histories could be distinguished by genetical characters.

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