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Annotated checklist of the umagillid turbellarians infesting echinoids (Echinodermata)

Gilles Doignon[1] **and Tom Artois**[2]

[1] **Laboratoire de Biologie Marine (CP 160/15), Université Libre de Bruxelles, 50 avenue F. D. Roosevelt, B-1050 Bruxelles, Belgium**

[2] **Hasselt University, Centre for Environmental Sciences, Research Group Biodiversity, Phylogeny & Population Studies, Agoralaan Gebouw D, B-3590 Diepenbeek, Belgium**

Corresponding author : G. Doignon, e-mail : gdoignon@gmail.com

ABSTRACT. A literature survey of the taxonomically complex taxon *Syndesmis* Silliman, 1881 is presented, resulting in the recognition of 22 valid species and three species mentioned in several works but not yet described. For each of these species the host(s) are mentioned and the distribution is given. These results are compared with earlier checklists and the differences are discussed.

KEY WORDS : Biogeography, *Marcusella*, symbiosis, *Syndesmis*, *Syndisyrinx*, Turbellaria.

INTRODUCTION

The family Umagillidae Wahl, 1910 (Platyhelminthes, Rhabdocoela) is the largest taxon of symbiotic turbellarians. It includes 68 valid species (WESTERVELT, 1981; CANNON, 1982, 1987; SHINN, 1987; CANNON, 1990; HERTEL et al., 1990; JANGOUX, 1990; KOZLOFF & WESTERVELT, 1990; WESTERVELT & KOZLOFF, 1990, 1992; MOENS et al., 1994; JONDELIUS, 1996; KOZLOFF, 1997; VASS & NAPPI, 1998). Most umagillids are common endosymbionts of echinoderms, particularly echinoids and holothuroids, and a few occur in sipunculids (see CANNON, 1982; JANGOUX, 1990). Our knowledge of the biology of umagillids is, however, very scant. For instance, although they are frequently found in the digestive tract or coelomic cavity of their hosts, almost nothing is known about the nature of their symbiotic relationships. The life cycle itself is completely elucidated for only four species : *Anoplodium hymanae* Shinn, 1983 and *Wahlia pulchella* Kozloff & Shinn, 1987 (both infesting holothuroids) (SHINN, 1983a, 1985a, b, 1986a), *Fallacohospes inchoatus* Kozloff, 1965 (infesting crinoids) (SHINN, 1986b) and *Syndesmis franciscana* (Lehman, 1946) (infesting echinoids) (SHINN, 1980, 1981, 1983b). Most umagillid species are host-specific, though a few apparently infest several, often phylogenetically unrelated, echinoderm species (see CANNON, 1982; SHINN, 1984; JANGOUX, 1990).

Research on the biology of these worms is greatly hampered by the complex taxonomy of the group, which often leads to wrong assumptions. For instance, for almost sixty years all umagillids found in echinoids were attributed to *Syndesmis echinorum* François, 1886 (see VON GRAFF, 1903). Although already very early on, it was suggested that more species existed (see BRAUN, 1889), it was not until recently that *S. echinorum* was split into six valid species (see KOZLOFF & WESTERVELT, 1987, 1990; WESTERVELT & KOZLOFF, 1990, 1992; KOZLOFF, 1997). After the description of the second recognized species of *Syndesmis*, *S. franciscana* (Lehman, 1946), many more species were described and some redescribed. Yet, authors often did not agree on the taxonomic importance of many characters. For instance, the validity of the genera *Syndisyrinx* Lehman, 1946 and *Marcusella* Westblad, 1953 has been the subject of many impassioned debates (LEHMAN, 1946; MARCUS, 1949; STUNKARD & CORLISS, 1951; WESTBLAD, 1953; HYMAN, 1960; CANNON, 1982, 1987; KOZLOFF & WESTERVELT, 1987, 1990; HERTEL et al., 1990; WESTERVELT & KOZLOFF, 1990, 1992). In the most recent literature, all umagillid species infesting echinoids were brought together into the genus *Syndesmis* Silliman, 1881 (see CANNON, 1982; MOENS et al., 1994; GEVAERTS et al., 1995; JONDELIUS, 1996).

Taxonomic literature regarding the species of *Syndesmis* has become extremely entangling, and is almost inaccessible for novice and even experienced researchers who are not particularly interested in taxonomy. As a result, several attempts were made to review the extensive literature on these animals : STUNKARD & CORLISS (1951), HICKMAN (1956), JENNINGS (1971), BAREL & KRAMERS (1977), CANNON (1982), HERTEL et al. (1990), JANGOUX (1990), VASS & NAPPI (1998). Yet, in recent years, several works (KOZLOFF & WESTERVELT, 1987, 1990; HERTEL et al., 1990; WESTERVELT & KOZLOFF, 1990, 1992; KOZLOFF, 1997) showed that many specimens previously attributed to a given species, in fact belong to several distinct species and, consequently, some species are less opportunistic than previously thought, thereby making most earlier checklists outdated. Moreover, because of confusing synonymies, discrepancies in the spelling of species names, and because of an incomplete literature survey or bad translations of non-English literature, these reviews contain mistakes and contradictory information.

The new checklist we present here is intended to give an overview of all umagillid species infesting echinoids, based on a complete literature survey. As the names of

many species changed through time, because these were synonymized, misidentified or even misspelled, it is quite difficult to understand the literature in a way other than chronologically. Only a detailed reappraisal of all descriptions allows to attribute the most recently accepted name to species misidentified in older works, for example the "*S. echinorum*" of BAREL & KRAMERS (1970) that was later described as *S. albida* Kozloff & Westervelt, 1990 and *S. rubida* Kozloff & Westervelt, 1990. In this work, we follow the most modern views, e.g. the one that considers *Syndisyrinx* a synonym of *Syndesmis* (MOENS et al., 1994; GEVAERTS et al., 1995; JONDELIUS, 1996). Similarly, we use the most recently published taxonomy of the echinoids (SMITH, 2003).

RESULTS AND DISCUSSION

To date, the 22 valid and three undescribed species of *Syndesmis* are known to infest a total of 31 species of echinoids belonging to the orders Clypeasteroida and Spatangoida (irregular sea urchins), Diadematoida, Echinoida and Temnopleuroida (regular sea urchins) (Table 1). The taxon *Syndesmis* occurs in European waters (from the Mediterranean Sea to the Barents Sea), the Caribbean, the entire Pacific Ocean and the Indian Ocean. Some echinoid species (e.g., *Echinometra oblonga* (de Blainville, 1825)) may host up to three umagillid species and some species of *Syndesmis* are found in various (up to five) echinoid hosts. Interestingly, some species are found in hosts belonging to distinct families or even orders. For instance, *S. echinorum* is found in *Paracentrotus lividus* (Lamarck, 1816) (Echinidae) as well as *Sphaerechinus granularis* (Lamarck, 1816) (Toxopneustidae).

The superscript numbers following the species names in our checklist (Table 1) refer to major discrepancies with previous checklists, the details of which are presented here :

(1) : Based on a literature survey, JANGOUX (1990) mentioned the occurrence of *S. echinorum* in *Psammechinus microtuberculatus* (de Blainville, 1825). However, only VON GRAFF (1903) has studied this species of sea urchin (from Trieste, Italy) and he reported that all 30 specimens he inspected were uninfested. Apart from the records presented in Table 1, MEIXNER (1926) mentioned the occurrence of *S. echinorum* in sea urchins from Lessin Island (Croatia), but without specifying the host.

(2) : VON GRAFF (1903) mentioned the occurrence of *Syndesmis echinorum* in *Strongylocentrotus droebachiensis* (Müller, 1776). This is impossible to verify owing to the lack of material. However, the fact that this species of echinoids is known to host two other morphologically similar and well documented species of *Syndesmis*, *S. franciscana* and *S. inconspicua* Westervelt & Kozloff, 1992 (see SHINN, 1984; WESTERVELT & KOZLOFF, 1992), suggests that the species VON GRAFF (1903) observed was probably not *S. echinorum*. VON GRAFF (1903) also reported *S. echinorum* in *Sphaerechinus granularis* from Bergen (Norway), but as this species of sea urchins is limited from the Mediterranean to the south of the English Channel, this observation is clearly erroneous. He probably misidentified the echinoid species, which could be *Echinus esculentus* Linnaeus, 1758, which harbours two distinct umagillid species (*S. rubida* and *S. albida*, see remarks 7 and 8).

(3) : Originally, *Syndesmis franciscana* was described as *Syndisyrinx franciscanus* (LEHMAN, 1946; SHINN, 1980), but was also mentioned as *Syndesmis franciscanus* (GIESE, 1958) and *Syndesmus franciscus* (BERGER & PROFANT, 1961). We regard *Syndesmis franciscana* as the correct name of this species, the genus name being feminine.

(4) : *Syndesmis antillarum* Stunkard & Corliss, 1951 was sometimes confused with *S. franciscana* (WESTBLAD, 1953; BARNES, 1969). Before its description, the species was also mentioned as *Syndesmus* sp. (POWERS, 1935). See also remark 9 about *S. collongistyla* Hertel et al., 1990.

(5) : *Syndesmis dendrastrorum* Stunkard & Corliss, 1951, *S. atriovillosa* Westblad, 1953 and *S. pallida* Hickman, 1956 were previously attributed to *Marcusella* (WESTBLAD, 1953; HICKMAN, 1956), a genus synonymized with *Syndesmis* by CANNON (1982). The first species is reported as *S. dendrastomum* in JANGOUX (1990).

(6) : *Syndesmis compacta* Komschlies & Vande Vusse, 1980, *S. mammilata* Komschlies & Vande Vusse, 1980, *S. philippinensis* Komschlies & Vande Vusse, 1980 and *S. alcalai* Komschlies & Vande Vusse, 1980 are treated here as valid despite of their incomplete species descriptions. The second species is reported as *S. mammillata* in JANGOUX (1990).

(7) : For a long time, *Syndesmis albida* and *S. rubida* were confused with *Syndesmis echinorum* (BAREL & KRAMERS, 1970, 1977), also reported as *Syndesmus echinorum* (SHIPLEY, 1901). It is impossible to know if WESTBLAD (1926), BRUCE et al. (1963) and LYONS (1973) observed *S. rubida* or *S. albida*. See also remark 8.

[a] This list updates previous reviews and reattributes outdated taxonomic names used in original works to the valid species. Superscript numbers following species names refer to notes in Results and Discussion.

Umagillid species : Some species have been described as *Syndisyrinx* or *Marcusella* by various authors but, without complete reappraisal of the group, validity of these genera is still matter of discussion. All species are thus attributed to the genus *Syndesmis*. Species are presented in the chronological order of their description.

Sea urchin host : Species in bold are irregular sea urchins. Synonyms : *Echinus esculentus* is also known in the literature on umagillids as *Echinus sphaera*; *Paracentrotus lividus* as *Toxopneustes lividus* or *Strongylocentrotus lividus*; *Strongylocentrotus pallidus* as *S. echinoides*. Locality : BS Barents Sea; C Caribbeans; EA East Atlantic; EP East Pacific; IO Indian Ocean; M : Mediterranean Sea; WP West Pacific.

References : "/" separates the authors having studied the species in the different localities mentioned. "?" is used when the species mentioned by the author is not clearly identified but probably belongs to the one named in this list. Authors in bold are the authority to which to refer for the original description of the species.

TABLE 1

List of the umagillids infesting sea urchins, with details about host species infested, localities and references.[a]

Umagillid species	Sea urchin host	Locality	References
Syndesmis echinorum[1]	*Paracentrotus lividus*	M : Banyuls (France) / Marseille (France) / EA : Roscoff (France) / Galicia (Spain)	**François, 1886**; Kozloff & Westervelt, 1987; Pers. obs. / Briot, 1906 / Cherbonnier, 1951; Barel & Kramers, 1970?; Pers. obs. / Lamas Seco & Rodriguez Babio, 1978; Cifrian et al., 1992; Pers. obs.
	Sphaerechinus granularis	M : Naples (Italy) / Trieste (Italy), Umag (Croatia) / Marseille (France) / Banyuls (France)	Russo, 1895; Wahl, 1909 / von Graff, 1903 / Briot, 1906 / Kozloff & Westervelt, 1987; Pers. obs.
	Strongylocentrotus droebachiensis?[2]	BS : Alexandrowsk (Russia)	von Graff, 1903
	Psammechinus miliaris	EA : Galicia (Spain)	Lamas Seco & Rodriguez Babio, 1978
Syndesmis franciscana[3]	*Strongylocentrotus franciscanus*	EP : California	**Lehman, 1946**; Giese, 1958; Jennings & Mettrick, 1968; Barnes, 1969; Mettrick & Jennings, 1969; Hertel et al., 1990
	Strongylocentrotus pallidus	EP : Washington State	Orihel, 1952; Shinn, 1980?, 1981, 1983b, 1984; Shinn & Cloney, 1986
	Strongylocentrotus droebachiensis	EP : Washington State	Shinn, 1980?, 1981, 1983b, 1984; Shinn & Cloney, 1986; Westervelt & Kozloff, 1992; Shinn, 1993
	Strongylocentrotus purpuratus	EP : California	Lehman, 1946?; Giese, 1958; Barnes, 1969; Mettrick & Jennings, 1969; Mettrick & Boddington, 1972; Holt & Mettrick, 1975; Hertel **et al.**, 1990
	Lytechinus anamesus	EP : California	Barnes, 1969; Hertel **et al.**, 1990
Syndesmis antillarum[4]	*Diadema antillarum*	C : Dry Tortugas, Florida / Bermuda / Unknown	Powers, 1935; **Stunkard & Corliss, 1951** / Snyder, 1980 / Westblad, 1953
Syndesmis dendrastrorum[5]	***Dendraster excentricus***	EP : California / Washington State	**Stunkard & Corliss**, 1950, **1951**; Smith, 1973 / Orihel, 1952; Shinn, 1981, 1984, 1988
Syndesmis atriovillosa[5]	***Spatangus purpureus***	EA : Plymouth (UK)	**Westblad, 1953**
Syndesmis punicea	*Heliocidaris erythrogramma*	WP : Tasmania / Sydney	**Hickman, 1956** / McRae, 1959?; Rohde & Watson, 1988
	Amblypneustes ovum	WP : Tasmania	Hickman, 1956
Syndesmis pallida[5]	***Echinocardium cordatum***	WP : Tasmania	**Hickman, 1956**
Syndesmis glandulosa	*Diadema setosum*	IO : Madagascar / WP : Philippines	**Hyman, 1960** / Komschlies & Vande Vusse, 1980a
	Echinothrix calamaris	WP : Philippines / IO : Seychelles	Komschlies & Vande Vusse, 1980a / Martens & De Clerck, 1994
Syndesmis evelinae	Unknown, *Echinometra lucunter*	C : Saint-Barthélémy	**Marcus, 1968**; Hertel **et al.**, 1990; Hertel & Duszynski, 1991
Syndesmis compacta[6]	*Echinometra oblonga*	WP : Philippines	**Komschlies & Vande Vusse, 1980a**
Syndesmis mammilata[6]	*Echinometra oblonga*	WP : Philippines	**Komschlies & Vande Vusse, 1980b**
Syndesmis philippinensis[6]	*Echinometra oblonga*	WP : Philippines	**Komschlies & Vande Vusse, 1980b**
Syndesmis alcalai[6]	*Heterocentrotus mammillatus*	WP : Philippines	**Komschlies & Vande Vusse, 1980b**
Syndesmis aethopharynx	*Paracentrotus lividus*	M : Banyuls (France)	**Westervelt & Kozloff, 1990**; Pers. obs.
Syndesmis albida[7]	*Echinus esculentus*	EA : Plymouth (UK), Roscoff (France)	Barel & Kramers, 1970; **Kozloff & Westervelt, 1990**
Syndesmis rubida[7, 8]	*Echinus esculentus*	EA : Plymouth (UK), Roscoff (France)	Geddes, 1880?; Silliman, 1881?; Cuénot, 1892?, 1900? (Roscoff); Shipley, 1901? (Plymouth); Barel & Kramers, 1970; **Kozloff & Westervelt, 1990**
Syndesmis collongistyla[9]	*Echinometra lucunter*	C : Saint-Barthélémy, Jamaica	**Hertel et al., 1990**
	Echinometra viridis	C : Jamaica	Nappi & Crawford, 1984; Hertel et al., 1990
	Lytechinus variegatus	C : Jamaica / Puerto Rico / Haiti	Jennings & Mettrick, 1968; Mettrick & Jennings, 1969; Nappi & Crawford, 1984; Allison et al., 1987; Ubelaker et al., 1988; Hertel et al., 1990; Vass & Nappi, 1998 / Hyman, 1960; Jones & Canton, 1970 / Jones & Canton, 1970
	Lytechinus williamsi	C : Jamaica	Hertel **et al.**, 1990
	Tripneustes ventricosus	C : Puerto Rico	Jones & Canton, 1970
Syndesmis inconspicua[10]	*Strongylocentrotus droebachiensis*	EP : Washington State	Orihel, 1952?; Shinn, 1981?, 1983b?, 1984?; **Westervelt & Kozloff, 1992**
	Strongylocentrotus pallidus?	EP : Washington State	Shinn, 1981?, 1983b?, 1984?
Syndesmis neglecta[11]	*Allocentrotus fragilis*	EP : Washington State / California	Berger & Profant, 1961?; **Westervelt & Kozloff, 1992** / Giese, 1958; Boolootian et al., 1959?; Hyman, 1960
Syndesmis longicanalis	*Tripneustes gratilla*	IO : Kenya	Moens & Martens, 1992; Gevaerts et al., 1993; **Moens et al., 1994**; Gevaerts et al., 1995
	Toxopneustes pileolus	IO : Kenya	Moens & Martens, 1992; Gevaerts et al., 1993; Moens et al., 1994; Gevaerts et al., 1995
Syndesmis cannoni	***Ammotrophus arachnoides***	IO : Western Australia	**Jondelius, 1996**
Syndesmis echiniacuti[12]	*Echinus acutus*	M : Banyuls, Port-Vendres (France)	François, 1886; **Kozloff, 1997**
Syndesmis sp 1	*Evechinus chloroticus*	WP : New Zealand	McRae, 1959
Syndesmis sp 2[13]	*Strongylocentrotus franciscanus*	EP : California	Lehman, 1946; Barnes, 1969; Mettrick & Jennings, 1969
	Strongylocentrotus purpuratus	EP : California	Barnes, 1969; Mettrick & Jennings, 1969
	Lytechinus anamesus	EP : California	Barnes, 1969; Mettrick & Jennings, 1969
Syndesmis sp 3	*Diadema savigny*	IO : Kenya	Martens & De Clerck, 1994

(8) : *Syndesmis rubida* can be distinguished from *S. albida* by the colour : the former is brown red while the latter is pale pink to white (KOZLOFF & WESTERVELT, 1990). According to their descriptions, GEDDES (1880), SILLIMAN (1881), CUÉNOT (1892, 1900) and SHIPLEY (1901) likely observed *S. rubida*.

(9) : Prior to its description, *Syndesmis collongistyla* was confused with *S. franciscana* and *S. antillarum* (JENNINGS & METTRICK, 1968 ; JONES & CANTON, 1970 ; NAPPI & CRAWFORD, 1984 ; ALLISON et al., 1987).

(10) : *Syndesmis inconspicua* was mentioned as *S. "echinorum"* in older literature (ORIHEL, 1952 ; SHINN, 1981, 1983b, 1984). This species was reported in *Strongylocentrotus droebachiensis* and *S. pallidus* (Sars, 1871) but not described until WESTERVELT & KOZLOFF (1992). These authors investigated specimens from *S. droebachiensis* only.

(11) : *Syndesmis neglecta* Westervelt & Kozloff, 1992 was previously listed as *Syndesmis franciscanus* (see GIESE, 1958), *Syndesmus franciscanus* (BOOLOOTIAN et al., 1959), *Syndesmis franciscana* (HYMAN, 1960) and *Syndesmus franciscus* (BERGER & PROFANT, 1961).

(12) : Specimens of *Syndesmis echiniacuti* Kozloff, 1997 were perhaps also used by FRANÇOIS (1886) in the original description of *Syndesmis echinorum* (see KOZLOFF & WESTERVELT, 1987 and KOZLOFF, 1997).

(13) : *Syndesmis* sp. 2 could be *S. inconspicua*. BARNES (1969) stated its close similarity with *S. echinorum*.

We hope this survey will be a useful tool for further research on this ecologically important group. Recent investigations have demonstrated that literature accounts of intraspecific variation in *Syndesmis* species found in distinct hosts or from distant locations should be treated sceptically, as some of these cases may in fact be instances of interspecific variation.

Re-evaluation of the current species, and the description of new species should be based on a thorough morphological study of the taxon as a whole (including the re-examination of all material deposited in collections), combined with molecular data. Unfortunately, confusions and misidentifications have persisted for years because some works were based on material of poor quality and sometimes lacked the study of histological sections. In some cases, researchers described a species, but failed to deposit type material in a collection. As a consequence, comparison between species can be very difficult, if not impossible, unless new material is collected. Yet, with the updated checklist presented here, future researchers will have immediate access to literature and a complete overview of *Syndesmis* species and their corresponding host(s) and geographical distribution.

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