



Current knowledge on Coralliophilidae (Gastropoda) and phylogenetic implication of anatomical and reproductive characters

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KEY WORDS: Gastropoda, Coralliophilidae, feeding, anatomy, sexual strategy, parental care, protoconch, phylogenetic relationships.

ABSTRACT

The current knowledge about feeding, anatomy, sexual strategy, parental care and protoconch of Coralliophilidae (Gastropoda) is reviewed. A preliminary cladistic analysis is carried out in order to unravel the phylogenetic relationship within Coralliophilidae and among Coralliophilidae and Muricidae. Twenty five characters and 55 character states chiefly relative to the anatomy, reproductive biology and larval development has been used in the analysis. The main result of the analysis is the separation of Coralliophilidae and Muricidae into two independent monophyletic clades, and the division of Coralliophilidae into a primitive clade represented by *Coralliophila squamosa*, with no known synapomorphies, and a more derived one, which give rise to three evolutionary lines represented by the genera *Babelomurex*, *Coralliophila* and *Leptoconchus*. This latter clade is characterised by the synapomorphy of brood care and by further four potential synapomorphies pertaining to the anatomy of the reproductive system. The internal relationships of Muricidae revealed by the present analysis support other current phylogenetic hypotheses obtained by analysis using anatomical or molecular characters. In conclusion, the paper stresses the necessity in deepening in the study of the anatomy and biology of coralliophilids, in particular in the reproductive system and reproductive strategy, since these aspects have been shown to be important in establishing internal relationships of coralliophilids.

RIASSUNTO

Viene riportata una revisione delle conoscenze attualmente disponibili su strategie alimentari e sessuali, anatomia, cure parentali e protoconche delle Coralliophilidae. Un'analisi cladistica preliminare è condotta col fine di dipanare le relazioni filogenetiche all'interno del gruppo e tra le Coralliophilidae e Muricidae. Sono stati usati nell'analisi venticinque caratteri per 55 stati, principalmente relativi all'anatomia, alla biologia riproduttiva e allo sviluppo larvale. Il risultato principale dell'analisi è la separazione di Coralliophilidae e Muricidae in due linee monofiletiche indipendenti, e la divisione delle Coralliophilidae in una linea primitiva rappresentata da *Coralliophila squamosa*, ed un clado più evoluto che ha dato origine a tre linee rappresentate dai generi *Babelomurex*, *Coralliophila* e *Leptoconchus*. Quest'ultimo clado è caratterizzato dalla sinapomorfia dell'incubazione delle capsule ovigere e da ulteriori quattro potenziali sinapomorfie riguardanti l'anatomia dell'apparato riproduttore. Le relazioni interne ai Muricidae rivelate da quest'analisi supportano altre ipotesi filogenetiche correnti derivate da dati anatomici e molecolari. In conclusione, il lavoro evidenzia la necessità di un approfondimento nello studio dell'anatomia e della biologia dei coralliofilidi, in particolare per ciò che riguarda l'apparato riproduttore e le strategie riproduttive, in quanto questi aspetti hanno dimostrato la loro importanza nello stabilire le relazioni interne tra i coralliofilidi.

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INTRODUCTION

Coralliophilids are marine neogastropods that live in tropical to temperate waters and feed exclusively on anthozoans. Up to date about 200 recent species have been recognised and grouped into 10 genera (KOSUGE & SUZUKI, 1985; VAUGHT, 1989) according to shell and opercular characters. However, since the shell of coralliophilids shows a great interspecific and intraspecific heterogeneity, the current generic and specific classification has to be considered as provisional and awaits for a critical review that should consider anatomical, reproductive, developmental and ecological aspects, on which scarce data exist. The lack of information on these aspects also has made it difficult to unravel the relationship of coralliophilids with other neogastropod families. Traditionally, Coralliophilidae has been considered a group closely related to Muricidae (THIELE, 1929; PONDER, 1973) due to their similarity in shell characters and external anatomy. However, in a first attempt to assess the phylogenetic relationships of neogastropod families by means of a cladistic analysis based on characters of the alimentary tract, KANTOR (1996) failed to

demonstrate such affinity. This assumed close relationship between Muricidae and Coralliophilidae has been supported recently by the results of phylogenetic analysis using DNA sequences coding for cytochrome c oxidase I (HARASEWYCH *et al.*, 1997) and 12 S rDNA sequences (OLIVERIO & MARIOTTINI, 2001a). OLIVERIO & MARIOTTINI (2001a) even proposed to rank coralliophilids as a subfamily within Muricidae on the basis of the outcome of their phylogenetic analysis that revealed the coralliophilids as an evolutionary line within the Muricidae with Rapaninae being their sister taxon.

Since there are marked differences among coralliophilids and muricids with respect to the anatomy (KANTOR, 1995; RICHTER & LUQUE, in press), reproductive strategy (parental care: PONDER, 1973; ROBERTSON, 1976; sex change: RICHTER & LUQUE, in press) and protoconch (RICHTER & THORSON, 1975; ROBERTSON, 1976; SCHELTEMA & WILLIAMS, 1983; RIEDL, 2000), an independent phylogenetic analysis using these characters should be undertaken in order to contrast it with the results of the analysis based on molecular characters carried out by OLIVERIO



& MARIOTTINI (2001 a). With this in mind, the present paper reviews the available information about feeding, anatomy, sexual strategy, parental care and protoconch of Coralliophilidae and carries out a cladistic analysis. Results are discussed and useful research lines are pointed out.

METHODS

A cladistic analysis with 25 selected characters and 55 characters states (see Appendix 1) was performed, from own and bibliographic data. The Hennig86 programme was used in order to infer a most parsimonious hypothesis of the phylogenetic relationships among 7 coralliophilid and 18 muricid species with the available database (see Appendix 2). The states of multistate characters were left unordered and the outgroup criterion was used to determine the ancestral state of each character. Two buccinoideans (*Nassarius vibex* and *Buccinum undatum*) were selected as outgroup. The analysis yielded 30 equally parsimonious trees from which a single consensus tree with 43 steps (ci 67; ri 85) was derived and discussed.

RESULTS AND DISCUSSION

Feeding

The anthozoans as food resource have been successfully exploited by coralliophilids, since they feed on seven anthozoan orders, namely Actiniaria, Scleractinia, Zoanthidea, Corallimorpharia, Antipatharia, Alcyonacea and Gorgonacea (Tab. 1). The preferred order of anthozoans is the Scleractinia, on which ca. 70% of the Recent species with known ecology and belonging to 7 genera feed. The degree of prey/host dependence varies widely within the family, which includes from ectobiotic mobile euryphagous species that feed on more than one order of anthozoans to endobiotic sessile stenophagous species which lack operculum and live embedded in the skeleton of hermatypic corals. Stenophagous coralliophilids, either ectobiotic or endobiotic, feeding only on one order of anthozoans, make about 85% of the species, and four genera are host specific (Tab. 1). The latter include the genera *Leptoconchus* and *Magilus*, whose species live exclusively associated to scleractinians corals, and *Rapa* and *Rhizochilus*, which are only found on soft corals (Alcyonacea) (LORENZ, 1996; OKUTANI, 2000) and black corals (Antipatharia) (KAY, 1979; POORMAN, 1981; KOSUGE & SUZUKI, 1985; OKUTANI, 2000), respectively. In stenophagous species, the shell shape is usually adapted to the anthozoan host on which they feed. This is the case of a few species that live attached to the surface of gorgonians (ALBERGONI & SPADA, 1972; POPPE & GOTTO, 1991), black corals (POORMAN, 1981; KOSUGE & SUZUKI, 1985) or massive hermatypic corals (MAES, 1967), or of those living buried inside the skeleton of hermatypic corals (MASSIN, 1982). However, adaptation of the shell to the host might also occur in euryphagous species, like for example in *Coralliophila meyendorffii* (OLIVERIO, 1989 a; OLIVERIO & MARIOTTINI, 2001 b).

Some associations of Recent coralliophilids with corals are very ancient in origin, dating back to the Paleogene. Endobiotic *Leptoconchus* species living inside the skeleton of faviid corals have existed at least since the upper Oligocene, and the associa-

tion between the epibiotic *Galeropsis* (= *Quoyula*) species and Pocilloporidae at least dates back to the Lower Miocene (LOZOUET & RENARD, 1998). A fossil species of *Coralliophila* from the Lower Oligocene has been also found living endobiotically inside *Cladocora* (Faviidae) (LOZOUET & RENARD, 1998). Due to poor fossilization, associations of coralliophilids with anthipatarians or gorgonaceans are unknown. Anthipatarians apparently arose during the Miocene (WELLS & HILL, 1956), hence the association of coralliophilids and black corals might be more recent than those between endobiotic coralliophilids and hermatypic corals. As gorgonaceans have existed since the Cretaceous (BAYER, 1956), the association of coralliophilids and gorgonians might have arisen earlier than that with antipatharians. When the associations between actiniids, zoanthids, corallimorpharians and soft corals appeared is almost impossible to determine since these anthozoans lack any type of skeleton or have a skeleton formed by loose spicules embedded in a fleshy cenenchime, and do not fossilise easily.

The specialized anatomical and biological features of coralliophilids (see below) and the long lasting (presumably more than 38 my) association with anthozoans suggest that such characters may reflect adaptations to their particular mode of life. It would be therefore interesting to find out whether coralliophilids feeding on a particular group of anthozoans show specific and common adaptations, and if so, whether these particular adaptations have evolved independently as a result of convergent evolution in species feeding on the same group of anthozoans or whether they have evolved in a single evolutionary line within coralliophilids. This should be best analysed in the framework of a phylogenetic study using anatomical, reproductive, developmental or even molecular characters, in which food type should then be plotted on the resulting tree topology. The results of such an analysis would show whether food type implies or not phylogenetic affinity among species or genera or, in other words, if there is a coevolution between coralliophilids and anthozoans.

Anatomy

Coralliophilids are characterised by the lack of jaws and radula (THIELE, 1929; GOHAR & SOLIMAN, 1963; WARD, 1965; PONDER, 1973; MASSIN, 1987, 1990; KANTOR, 1995), and by a more or less long pleurembolic proboscis that acts as a sucking bomb and is adapted to penetrate, predigest and suck the soft tissue of their preys (WARD, 1965; KANTOR, 1995). Further features, such as the absence of accessory salivary glands, whose presence is considered a synapomorphy of neogastropods (PONDER, 1973; HARASEWYCH, 1984; TAYLOR & MORRIS, 1988; KANTOR, 1996; but see PONDER & LINDBERG, 1997), or the absence of dorsal glandular folds of the oesophagus and the fusion of the paired salivary ducts into a single duct are considered as characteristic for the group by KANTOR (1995, 1996), who assumed coralliophilids to be uniform at least in respect to the alimentary tract. However, the loss of accessory salivary glands is a tendency in the evolution of Neogastropoda and occurs in many groups, including Muricidae (WU, 1973; KOOL, 1993 a), Buccinoidea, Vasidae, Harpidae, Mitridae, Columbari-



Table 1. Anthozoan preys of Coralliophilidae. **Abbreviations:** A, Antipatharia; Ac, Actiniaria; Al, Alcyonaria; C, Corallimorpharia; G, Gorgonacea; S, Scleractinia; Z, Zoanthidea.

| Species | S | G | C | A | Ac | Z | Al | References |
|---|---|---|---|---|----|---|----|--|
| <i>Babelomurex benoiti</i> (Tiberi, 1855) | | | | | | | + | Barrajón, pers. com. |
| <i>Babelomurex cariniferus</i> (Sowerby, 1834) | + | | | | | | | SPADA, 1968; GHISOTTI & SPADA, 1970; CHEMELLO, 1986; RICHTER & LUQUE, in press |
| <i>Babelomurex fearnleyi</i> (Emerson & D'Attilio, 1965) | + | | | | | | | OKUTANI, 2000 |
| <i>Babelomurex bindsi</i> (Carpenter, 1857) | + | | | | | | | GLYNN & WELLINGTON, 1983 |
| <i>Babelomurex oldroydi</i> (Oldroyd, 1929) | | | + | | | | | WICKSTEN & WRIGHT, 1993 |
| <i>Coralliobia cumingii</i> (H. & A. Adams, 1863) | | | | + | | | | D'ATTILIO & KOSUGE, 1988 |
| <i>Coralliobia fimbriata</i> (A. Adams, 1854) | + | | | | | | | OKUTANI, 2000 |
| <i>Coralliophila abbreviata</i> (Lamarck, 1816) | + | | + | | | + | | WARD, 1965; OTT & LEWIS, 1972; MILLER, 1972, 1981; WELLS & LALLI, 1977; HAYES, 1990 |
| <i>Coralliophila adansoni</i> (Kosuge & Fernandes, 1989) | | | | | | | + | ROLÁN & FERNANDES, 1990 |
| <i>Coralliophila brevis</i> (Blainville, 1832) | | + | | | | | | ALBERGONI & SPADA, 1969, 1972; SABELLI & SPADA, 1980; POPPE & GOTO, 1991; RICHTER & LUQUE, in press |
| <i>Coralliophila bulbiformis</i> (Conrad, 1837) | + | | | | | | | KOSUGE & SUZUKI, 1985; OKUTANI, 2000 |
| <i>Coralliophila caribaea</i> Abbott, 1958 | + | + | + | | | + | | MILLER, 1972, 1981; WELLS & LALLI, 1977 |
| <i>Coralliophila clatibrata</i> (A. Adams, 1854) | | | | | | + | | ROBERTSON, 1981; RIVAS & JAY, 1996 |
| <i>Coralliophila costularis</i> (Lamarck, 1816) | + | | | | | | | KOSUGE & SUZUKI, 1985; LORENZ, 1996; OKUTANI, 2000 |
| <i>Coralliophila erosa</i> (Röding, 1798) | + | | | | | | | KAY, 1979; KOSUGE & SUZUKI, 1985; DRIVAS & JAY, 1996; OKUTANI, 2000 |
| <i>Coralliophila jeffreysii</i> E. A. Smith, 1879 | + | | | | | | | OKUTANI, 2000 |
| <i>Coralliophila kaofitorum</i> Vega, Vega & Luque, 2002 | | | | + | | | | VEGA, VEGA & LUQUE, 2002 |
| <i>Coralliophila meyendorffii</i> (Calcara, 1845) | + | | | | | + | | GARAVELLI & MELONE, 1968; SPADA, SABELLI & MORANDI, 1973; SPADA, 1979; CHEMELLO, 1986; LUQUE, 1986; OLIVERIO, 1989 b; PÉREZ Y MORENO, 1991; GARCÍA-RASO ET AL., 1992; CHINTIROGLOU & KOUKOURAS, 1992 |
| <i>Coralliophila morishimai</i> Kuroda & Shikama in Shikama, 1966 | | + | | | | | | KOSUGE & SUZUKI, 1985 |
| <i>Coralliophila neritoidea</i> (Lamarck, 1816) | + | | | | | | | MAES, 1967; ROBERTSON, 1970; KAY, 1979; KOSUGE & SUZUKI, 1985; SOONG & CHEN, 1991; LIN & LIU, 1995; LORENZ, 1996; DRIVAS & JAY, 1996 |
| <i>Coralliophila panormitana</i> (Monterosato, 1869) | | + | | | | + | | OLIVERIO, 1989 a; TEMPLADO <i>et al.</i> , 1993 |
| <i>Coralliophila radula</i> (A. Adams, 1855) | + | | | | | | | DRIVAS & JAY, 1996 |
| <i>Coralliophila richardi</i> (Fischer, 1882) | + | | | | | | | CECALUPO, 1984; BOUCHET & WARÉN, 1985; Luque, pers. obs. |
| <i>Coralliophila squamosa</i> (Bivona, 1838) | | | | | + | | | GARAVELLI & MELONE, 1968 (as <i>C. lamellosa</i>); OLIVERIO, 1989 b |
| <i>Coralliophila squamosissima</i> (E. A. Smith, 1876) | | | | | + | | | KOSUGE & SUZUKI, 1985; OKUTANI, 2000 |
| <i>Galeropsis madreporarum</i> (Sowerby, 1832) | + | | | | | | | GHISOTTI, 1968; KEEN, 1971; GLYNN, STEWART & McCOPPER, 1983; KAY, 1979; GUZMÁN, 1988; LOZOUET & RENARD, 1998; OKUTANI, 2000 |
| <i>Leptoconchus cumingii</i> Deshayes, 1863 | + | | | | | | | GOHAR & SOLIMAN, 1963; MASSIN, 1982 |
| <i>Leptoconchus cyphastreae</i> Massin, 1983 | + | | | | | | | MASSIN, 1983 |
| <i>Leptoconchus expositus</i> Shikama, 1963 | + | | | | | | | MASSIN, 1982; OKUTANI, 2000 (as <i>Magilus expositus</i>) |
| <i>Leptoconchus lamarckii</i> Deshayes, 1863 | + | | | | | | | GOHAR & SOLIMAN, 1963; MASSIN, 1982; OKUTANI, 2000 |
| <i>Leptoconchus peronii</i> (Lamarck, 1818) | + | | | | | | | GOHAR & SOLIMAN, 1963 (as <i>L. globosus</i>); MASSIN, 1982 (as <i>L. striatus</i>), 1990; OKUTANI, 2000 (as <i>L. striatus</i>) |
| <i>Leptoconchus rostratus</i> A. Adams, 1864 | + | | | | | | | MASSIN, 1982 |
| <i>Leptoconchus vangoetbemi</i> Massin, 1983 | + | | | | | | | MASSIN, 1983 |
| <i>Magilus antiquus</i> Montfort, 1810 | + | | | | | | | LAMY, 1923; MASSIN, 1982; DRIVAS & JAY, 1996; OKUTANI, 2000 |
| <i>Rapa incurva</i> (Dunker, 1853) | | | | | | | + | OKUTANI, 2000 |
| <i>Rapa rapa</i> (Linnaeus, 1758) | | | | | | | + | LORENZ, 1996; OKUTANI, 2000 |
| <i>Reliquiaecava robillardi</i> (Lienard, 1870) | + | | | | | | | MASSIN, 1987 |
| <i>Rhizocbilus anthipatum</i> Steenstrup, 1850 | | | | + | | | | KAY, 1979; KOSUGE & SUZUKI, 1985; OKUTANI, 2000 |
| <i>Rhizocbilus</i> sp. | | | | + | | | | POORMAN, 1981 |

Notes: ¹ Under laboratory conditions, it is uncertain if it is a prey under natural conditions.



dae and Marginellidae (PONDER, 1973). Besides, a preliminary study on Mediterranean coralliophilids reveals that the complete reduction of the accessory salivary glands is not the rule in Coralliophilidae (pers. obs.). The fusion of the ducts of the salivary glands and the loss of the dorsal glandular folds of the oesophagus also needs to be confirmed in other species. The first character occurs at least in *Coralliophila abbreviata* (WARD, 1965), *Babelomurex naskensis* and *Babelomurex sentix* (KANTOR, 1995), and *Coralliophila meyendorffii* and *Babelomurex cariniferus* (pers. obs.). The loss of the dorsal glandular folds of the oesophagus occurs in *Coralliophila abbreviata* (WARD, 1965) and in *Babelomurex naskensis* and *Babelomurex sentix* (KANTOR, 1995).

While at present the presumed uniformity of the feeding apparatus awaits for confirmation, the anatomical and histological organisation of the reproductive system is certainly quite variable within the group and is useful in establishing internal relationships within coralliophilids, as will be shown later. On the basis of available information on the reproductive system of four Mediterranean species, viz. *Coralliophila squamosa* (Bivona, 1838) (OEHLMANN, 1994), *Coralliophila meyendorffii* (Calcare, 1845), *Coralliophila brevis* (Blainville, 1832) and *Babelomurex cariniferus* (Sowerby, 1834) (RICHTER & LUQUE, in press) and

three Red Sea species, *Leptoconchus peronii* (= *globosus*) (Lamarck, 1818), *Leptoconchus cumingii* Deshayes, 1863 and *Magilopsis lamarckii* Deshayes, 1863 (GOHAR & SOLIMAN, 1963, included by MASSIN, 1982 in *Leptoconchus*), four basic types of reproductive system organisations within coralliophilids can be recognised. They differ from each other in the presence or absence of a gonopericardial duct, seminal receptacle (or sperm ingesting gland) or a slit in the proximal region of the prostata, in the secretory areas of the capsule gland, in the structure of the bursa copulatrix, in the grade of closure and the number of folds of the ventral channel, and in the shape of the penis and the albumen gland. Within the genus *Coralliophila* two of these four types occur, one shared by *Coralliophila meyendorffii* and *C. brevis*, while the other corresponds to *C. squamosa*. The reproductive system of the latter species resembles more closely to that of certain Ocenebrinae than to any of the other known coralliophilids, suggesting that the genus *Coralliophila* is polyphyletic. The third type of reproductive system is represented by the genus *Leptoconchus*, which apparently lack a proximal seminal receptacle (RICHTER & LUQUE, in press). Finally, the fourth type corresponds to *Babelomurex cariniferus*, whose reproductive system is similar to that of *Coralliophila meyendorffii* and *C. brevis*, but dif-

Table 2. Data on reproductive and life history strategy of coralliophilids. **Abbreviations:** **A**, aggregates; **b**, both sexes mobile; **D**, mode of development; **f**, females; **m**, males; **M**, mobility; **p**, planktotrophic; **PCF**, positive correlation between female fecundity and female size; **PF**, pseudopenis in females; **s**, sessile; **ss**, semisessile; **SSD**, sexual size dimorphism; **SR**, sex ratio; **v**, variable; +: presence of the character; ? no data available.

| Species | SR (m:f) | SSD | PF | A | PCF | M | D | References |
|-----------------------------------|------------------|----------------|----------------|---|-----|--------------------------|---|---|
| <i>Babelomurex cariniferus</i> | 1:1 ¹ | + | + | ? | + | b | p | RICHTER & LUQUE, in press |
| <i>Coralliophila abbreviata</i> | v | + | + | + | + | b | p | WARD, 1965; WELLS & LALLI, 1977; HAYES, 1990; FIORONI, OEHLMANN & STROBEN, 1991 |
| <i>Coralliophila brevis</i> | ? | ? ⁴ | + | ? | ? | ss ⁵ | ? | ALBERGONI & SPADA, 1972; RICHTER & LUQUE, in press |
| <i>Coralliophila caribaea</i> | 1:1 ¹ | + | ? | ? | + | b | p | WELLS & LALLI, 1977 |
| <i>Coralliophila meyendorffii</i> | 1:1 ¹ | + | + | ? | + | b | p | RICHTER & LUQUE, in press |
| <i>Coralliophila neritoidea</i> | >1 ² | + | + | + | + | b | p | SOONG & CHEN, 1991; LIN & LIU, 1995 (both references as <i>C. violacea</i>) |
| <i>Coralliophila squamosa</i> | ? | ? ⁴ | + | ? | ? | b | ? | OEHLMANN, 1994 (as <i>Coralliophila lamellosa</i>) |
| <i>Leptoconchus cyphastreae</i> | ? ⁸ | ? | ? | ? | ? | f: s, m: ? | ? | MASSIN, 1983 |
| <i>Leptoconchus cumingii</i> | ? | ? | ? | ? | ? | s | p | GOHAR & SOLIMAN, 1963 |
| <i>Leptoconchus lamarckii</i> | ? | ? | ? | ? | ? | s | p | GOHAR & SOLIMAN, 1963 (as <i>Magilopsis lamarckii</i>) |
| <i>Leptoconchus peronii</i> | 1:1 ³ | + | ? ⁵ | ? | ? | f: s, m: ss ⁷ | p | GOHAR & SOLIMAN, 1963 (as <i>L. globosus</i>); MASSIN, 1982 (as <i>L. striatus</i>), 1990 |
| <i>Leptoconchus vangoethemi</i> | ? ⁸ | ? | ? | ? | ? | f: s, m: ? | ? | MASSIN, 1983 |
| <i>Reliquiaecava robillardii</i> | ? ⁸ | ? | ? | ? | ? | f: s, m: ss/s | p | MASSIN, 1987 |
| <i>Rhizochilus</i> sp. | ? | ? | ? | + | ? | s | p | POORMAN, 1981 |

Notes: ¹ Sex ratio does not deviate significantly from the expected 1:1 Fischer sex ratio for dioic species.

² Males are significantly more abundant than females.

³ MASSIN (1990) did not reported about the sex ratio of the species, but a goodness of fit test performed with the frequency data reported in the paper reveals that male and female proportion did not depart significantly from the expected 1:1 ratio for dioic species.

⁴ Sample size was too small to test statistically sexual size dimorphism. Nevertheless, the smallest individual/s of the sample was/were males, suggesting the existence of sexual size dimorphism.

⁵ MASSIN (1990) observed a couple of males with vestigial penis, but since gonads were not examined microscopically, it cannot be ruled out that the individuals were in fact females. At least, the vestigial penis suggested that individuals might reduce penis as a consequence of sex change from male to female.

⁶ According to ALBERGONI & SPADA (1972) large individuals of *C. brevis* tend to attach firmly to the gorgonian on which they feed, while smaller individuals are mobile.

⁷ MASSIN (1982, as *L. striatus*) observed free living individuals of about 3 mm in shell length, which fall within the size range of males according to MASSIN (1990). Since MASSIN (1990) also observed males burrowed inside the coral skeleton, this means that males pass through a creeping stage before being sessile.

⁸ Males are virtually absent in the samples.



fers in the shape of the albumen gland and the penis, and in the number of folds and grade of closure of the ventral channel (RICHTER & LUQUE, in press). The common features of the reproductive system of these three species include among others the reduction of the dorsal lobe of the capsule gland and the existence of a large vestibule, both of which are potentially synapomorphies of a subgroup within coralliophilids, as will be discussed later. Whether the genus *Leptoconchus* and *Coralliophila squamosa* also presents these characters is still unclear and should be found out. Apparently, at least at the present stage of knowledge, there is no character of the reproductive system common for all coralliophilids except for the structure of the penis duct. This might be rather a consequence of the different degree of detail of the anatomical studies. More thorough anatomical studies on the reproductive system of additional species from each of these genera and of other genera not used in the analysis should be undertaken in order to define genera and to unravel relationships within coralliophilids.

Reproductive strategy

Although coralliophilids have been traditionally considered as dioic species (ROBERTSON, 1970; OLIVERIO, 1989 b), there are up to date no direct (histological) nor indirect evidences supporting this assumption. By contrast, the relatively high incidence of reduced penis in females of coralliophilids and the widespread sexual size dimorphism with males smaller than females rather points to the existence of protandry in coralliophilids, which has been definitely proved to occur in *C. meyendorffii* and *B. cariniferus* by the results of a laboratory monitoring of penis reduction coupled with an histological and anatomical study of the reproductive system of monitored individuals (RICHTER & LUQUE, in press). Other life history traits of coralliophilids, such as the tendency to form aggregates, sessility and dependence on a spatially discontinuously distributed food source have been linked in other prosobranchs to a special type of hermaphroditism called environmental sex determination (ESD). ESD has been observed in calyptraeids (HOAGLAND, 1978), eulimids (WARÉN, 1980, 1983) and giant territorial limpets (WRIGHT, 1989). Departures from the expected 1:1 sex ratio for dioecia, which are common in protandric species, are also found in coralliophilids. Samples with a very low proportion of males or with virtually absent males are common in coral boring species (MASSIN, 1983, 1987). This also occurs in sedentary protandric gastropods with a mobile male phase, like the sedentary turritellid *Vermicularia spirata* (BIELER & HADFIELD, 1990) and the non-gregarious *Crepidula dilatata* (GALLARDO, 1976). In *Coralliophila neritoides* (Lamarck, 1816) the sex ratio is skewed toward males (SOONG & CHEN, 1991), as is the rule in protandric species. In *Coralliophila abbreviata* (Lamarck, 1816) the sex ratio is variable depending on the geographical locality, and some populations have equal proportion of males and females, while in others males predominates (WELLS & LALLI, 1977; HAYES, 1989).

WARNER, ROBERTSON & LEIGH (1975) linked the correlation between fecundity and size or age to the sexual strategy of the species. According to the authors, if the fecundity of a sex

increases with size or age, sex change is advantageous over dioecia. In coralliophilids usually exists a positive correlation between female fecundity and female size. Hence, according to the hypothesis of WARNER, ROBERTSON & LEIGH (1975) protandry should be expected. An increase of female fecundity with female size has been reported in *C. neritoides* (LIN & LIU, 1995), *C. abbreviata* and *C. caribaea* (WELLS & LALLI, 1977) and also occur in *C. meyendorffii* and *B. cariniferus* (RICHTER & LUQUE, unpublished).

Table 2 summarises the available information about aspects of coralliophilid biology that has been related to protandry or ESD in other gastropods. Except for *Coralliophila meyendorffii* and *Babelomurex cariniferus*, in most of the species the sexual strategy has still to be assessed by using histological methods together with a field or laboratory monitoring of penis reduction (= sex change). This monitoring must follow an experimental design in order to test dependence of percentage of individuals reducing penis (= changing sex) on initial population structure, as such undertaken for calyptraeids by HOAGLAND (1978) and COLLIN (2000) and for coralliophilids by RICHTER & LUQUE (in press). In *Coralliophila meyendorffii* and *Babelomurex cariniferus* the evidences pointing to protandry includes direct observation of penis reduction, the existence of transitional sexual stages close to onset and during breeding season and sexual size dimorphism with males smaller than females (RICHTER & LUQUE, in press). In *Coralliophila neritoides* an environmental sex determination has been proposed (SOONG & CHEN, 1991), although it awaits for histological confirmation. In this species evidences pointing to ESD are sexual size dimorphism with males smaller than females, a skewed sex ratio toward males, the observed degeneration of the penis and the correlation of the smallest female size and the largest male size to aggregates structure. In *Coralliophila squamosa*, pseudohermaphroditism has been reported (FIORONI, OEHLMANN & STROBEN, 1991; OEHLMANN, 1994). However, this statement has to be checked because this conclusion is based on the observation of four females with pseudopenis histologically similar to male penis in a sample of six individuals (4 females: 2 males). Such fact does not rule out the existence of protandry.

Parental care

Contrary to most neogastropods, which lay benthic egg capsules, coralliophilids incubate their brood inside the female mantle cavity enclosed in membranous flat elliptical egg-pouches (GOHAR & SOLIMAN, 1963; GHISOTTI & SPADA, 1970; WELLS & LALLI, 1977; ROBERTSON, 1980; MASSIN, 1983, 1987, 1990; ROLÁN & FERNANDES, 1990; LIN & LIU, 1995; RICHTER & LUQUE, in press). Brooding mechanism, however, is not the same in all species. While *Coralliophila abbreviata*, *C. neritoides* and species of *Leptoconchus* breed loose unattached egg-capsules inside the pallial cavity until larvae are mature and ready to hatch, females of *Coralliophila caribaea* push the capsules they breed outside the pallial cavity while development proceeds, and attach them to a groove between foot and operculum (WELLS & LALLI, 1977). Besides, in *Leptoconchus* (GOHAR & SOLIMAN, 1963), *Coralliophila meyendorffii* and *Babelomurex cariniferus* (pers.



Table 3. Available data on protoconch, larval development, and bathymetrical and geographical distribution of coralliophilids. Data with ? are not included in the statistical test. **Abbreviations:** AD, area of distribution: A, Atlantic; AA, ampho-Atlantic; EA, East Atlantic; EP, East Pacific; I, Indian Ocean; IP, Indo-Pacific; M, Mediterranean; RS, Red Sea; P, Pacific Ocean; WP, West Pacific; BR, bathymetric range (exact depths in meters): b, bathyal; dw, deep-water; s, sublittoral; sm, seamounts; sw, shallow-water; MD, mode of development: p, planktotrophic; np, non planktotrophic; * inferred from protoconch; ** number of whorls of protoconch correspond to planktotrophic type, but lack of shell ornamentation points to non-planktotrophic development, no reliable inference can be made; *** number of whorls indicates non-planktotrophic development, but shell ornamentation points to planktotrophic one, no reliable inference can be made; ? inferred type of larval development doubtful, since shell ornamentation is eroded; NW, number of whorls of protoconch; P, type of protoconch, according numbers giving in text: e, protoconch completely or partially eroded; – no data available.

| Species | P | NW | MD | BR | AD | References |
|---|----------------|-------|-----|---------|----------|---|
| <i>Babelomurex cariniferus</i> (Sowerby, 1834) | 7 ¹ | 1.5 | p | s | EA, M | D'ATTILIO, 1972; GARCÍA-TALAVERA, 1983; KOSUGE & FERNANDES, 1988; RICHTER & LUQUE, in press |
| <i>Babelomurex cariniferoides</i> (Shikama, 1966) | 1 | 3 | p* | - | WP | KOSUGE, 1986 a; OKUTANI, 2000 |
| <i>Babelomurex centimanus</i> Kosuge, 1985 | 2 | 3 | p* | dw | WP | KOSUGE, 1985 b; KOSUGE & SUZUKI, 1985 |
| <i>Babelomurex cookae</i> Kosuge, 1988 | 1 | 2.5 | p* | 135–315 | EP | KOSUGE, 1988 a |
| <i>Babelomurex deburghiae</i> (Reeve, 1857) | 5 | 1.5–2 | np? | 20–200 | WP | KOSUGE, 1986 a; OKUTANI, 2000 |
| <i>Babelomurex fusiformis</i> (Martens, 1902) | e | 2 | np? | 486 | IP | AZUMA, 1973; KOSUGE & SUZUKI, 1985 |
| <i>Babelomurex glaber</i> Kosuge, 1998 | 7 | 2 | np* | 490 | I | KOSUGE, 1998 |
| <i>Babelomurex hirasei</i> (Shikama, 1964) | 7 | 2 | np* | - | WP | KOSUGE, 1986 a, d; OKUTANI, 2000 |
| <i>Babelomurex lischkeanus</i> (Dunker, 1882) | 3 | 3 | ** | - | I, WP | D'ATTILIO, 1972 (as <i>Latiaxis lischkeana</i>); KOSUGE & SUZUKI, 1985; KOSUGE, 1986 c |
| <i>Babelomurex memimuramai</i> Kosuge, 1985 | 6 | 1 | *** | dw | WP | KOSUGE, 1985 b |
| <i>Babelomurex miyokoeae</i> Kosuge, 1985 | 1 | 2.5 | p* | - | WP | KOSUGE, 1985 b |
| <i>Babelomurex squalida</i> Kosuge, 1985 | 1 | 2 | p* | - | WP | KOSUGE, 1985 b |
| <i>Babelomurex stenospinus</i> (Kuroda, 1961) | 5 | 2 | p* | 30–200 | WP | KOSUGE, 1986 a; OKUTANI, 2000 |
| <i>Babelomurex yamatoensis</i> Kosuge, 1986 | 4 | 2 | p* | dw | WP | KOSUGE, 1986 a; OKUTANI, 2000 |
| <i>Babelomurex yumimuramai</i> Kosuge, 1985 | 4 | 2 | p* | dw | WP | KOSUGE, 1985 b; KOSUGE & SUZUKI, 1985 |
| <i>Coralliophila abbreviata</i> (Lamarck, 1816) | - | - | p | sw, sm | WA | BANDEL, 1975; WELLS & LALLI, 1977 |
| <i>Coralliophila aberrans</i> (C. B. Adams, 1850) | 1 | 4.5 | p | sw, sm | WA | BANDEL, 1975; LEAL, 1991 |
| <i>Coralliophila adamsi</i> (Kosuge & Fernandes, 1989) | e | 1.5 | np? | sw | EA | KOSUGE & FERNANDES, 1989 (as <i>Ocenebrina adamsi</i>); ROLÁN & FERNANDES, 1990 |
| <i>Coralliophila caribaea</i> Abbott, 1958 | 1 | 4.5 | p | sw | WA | BANDEL, 1975; WELLS & LALLI, 1977; COSEL, 1982; JONG & COOMANS, 1988; LEAL, 1991 |
| <i>Coralliophila carnosa</i> Kosuge, 1986 | 1 | 3–4 | p* | sw | WP | KOSUGE, 1986 d; OKUTANI, 2000 |
| <i>Coralliophila clathrata</i> (A. Adams, 1854) | 1 | ca. 4 | p | sw | IP | YEN, 1935; ROBERTSON, 1980; KOSUGE & SUZUKI, 1985 |
| <i>Coralliophila flava</i> Kosuge, 1985 | 4 | 2 | p* | - | I, WP | KOSUGE, 1985 b |
| <i>Coralliophila kaofitum</i> Vega, Vega & Luque, 2002 | 1 | 3.5–4 | p* | 18–48 | EA | VEGA, VEGA & LUQUE, 2002 |
| <i>Coralliophila leucostoma</i> Kosuge, 1986 | e | 3 | p* | sw | WP | KOSUGE, 1986 b |
| <i>Coralliophila liltvedii</i> Kosuge, 1986 | 1 | 3 | p* | 245 | EA | KOSUGE, 1986 b |
| <i>Coralliophila meyerdorffii</i> (Calcar, 1845) | 1 | 4.25 | p | s | EA, M | RICHTER & THORSON, 1976; COSEL, 1982; RICHTER & LUQUE, in press |
| <i>Coralliophila mitraeformis</i> Kosuge, 1985 | 1 | 2.5 | p* | dw | WP | KOSUGE, 1985 b; OKUTANI, 2000 |
| <i>Coralliophila occidentale</i> Kosuge & Fernandes, 1988 | 1 | 4 | p* | 60 | EA | KOSUGE & FERNANDES, 1988 |
| <i>Coralliophila obmurai</i> Kosuge, 1985 | 4 | 2 | p* | 12 | WP | KOSUGE, 1985 b |
| <i>Coralliophila raramaculatus</i> Kosuge & Fernandes, 1989 | e | 2.5 | p? | 1 | EA | KOSUGE, 1989 |
| <i>Coralliophila richardi</i> (P. Fischer, 1882) | 1 | 4 | p* | b | AA, M | CECALUPO, 1984; TAVIANI & TAVIANI, 1986; BOUCHET & WARÉN, 1985 |
| <i>Coralliophila roseocephala</i> Kosuge, 1986 | 1 | 3–4 | p* | 200 | WP | KOSUGE, 1986 d; OKUTANI, 2000 |
| <i>Coralliophila tetragona</i> Kosuge, 1986 | e | 4 | p* | - | I | KOSUGE, 1986 b |
| <i>Galeropsis madreporarum</i> (Sowerby, 1832) | 1 | 4 | p | sw | IP | SCHELTEMA & WILLIAMS, 1983 |
| <i>Hirtomurex nakamurai</i> Kosuge, 1985 | 7 | 2 | np* | 150 | WP | KOSUGE, 1985 a; OKUTANI, 2000 |
| <i>Hirtomurex oyamai</i> Kosuge, 1985 | e | 2 | np? | 180 | WP | KOSUGE, 1985 a |
| <i>Hirtomurex vertigo</i> Kosuge, 1986 | e | 3 | p? | 120 | WP | KOSUGE, 1986 d |
| <i>Latiaxis latipinnatus</i> Azuma 1961 | 1 | 3 | p* | - | WP | KOSUGE & SUZUKI, 1985; KOSUGE, 1986 a |
| <i>Leptoconchus cumingii</i> Deshayes, 1863 | - | - | p | sw | RS, I | GOHAR & SOLIMAN, 1963; MASSIN, 1982 |
| <i>Leptoconchus lamarckii</i> (Deshayes, 1863) | - | - | p | sw | RS, I, P | GOHAR & SOLIMAN, 1963; MASSIN, 1982; OKUTANI, 2000 |
| <i>Leptoconchus peronii</i> (Lamarck, 1818) | - | - | p | sw | RS, I, P | GOHAR & SOLIMAN, 1963 (as <i>L. globosus</i>); MASSIN, 1983 (as <i>L. striatus</i>), 1990; OKUTANI, 2000 (as <i>L. striatus</i>) |
| <i>Mipus basicostatus</i> Kosuge, 1988 | 1 | ca. 3 | p* | - | I | KOSUGE, 1988 b |
| <i>Mipus botei</i> Kosuge, 1985 | 4 | 2 | p* | 160–190 | WP | KOSUGE, 1985 b; OKUTANI, 2000 |
| <i>Mipus intermedius</i> Kosuge, 1985 | 1 | 3 | p* | - | WP | KOSUGE, 1985 b; OKUTANI, 2000 |
| <i>Mipus ovoideus</i> Kosuge, 1985 | 7 | 2 | p* | - | WP | KOSUGE, 1985 b; OKUTANI, 2000 |
| <i>Mipus eugeniae</i> (Bernardi, 1853) | 7 | 2 | np* | - | WP | D'ATTILIO, 1972; KOSUGE & SUZUKI, 1985 |
| <i>Rapa rapa</i> (Linnaeus, 1758) | 1 | ca. 3 | p* | sw | I, P | D'ATTILIO, 1972 (as <i>Rapa papyracea</i>); KOSUGE & SUZUKI, 1985 |
| <i>Reliquiaecava robillardii</i> (Lienard, 1870) | e | 3 | p* | sw | I, P | MASSIN, 1982, 1987 |
| <i>Rhizochilus</i> sp. | 1 | 3 | p* | dw | EP | POORMAN, 1981 |

Notes: ¹ D'ATTILIO (1972) described a smooth and globose protoconch of 1½ whorls for *Babelomurex babelis* (a junior synonym of *B. cariniferus*), but our own observations prove that planktotrophic veligers hatched from egg-capsules.



obs.) the capsules with larvae ready to hatch are then freed outside the mantle cavity while in *C. caribaea* they remain attached to the foot through a filament. Differences in the breeding mechanism of gastropods exhibiting brood protection are usual. Vermetid females incubate egg-capsules loose inside the pallial cavity, or attached to the inner surface of the vermiform shell. The type of brooding is linked to the presence or absence of a slit in the mantle (MORTON, 1965), but it has little phylogenetic value in vermetids, since in many genera both types of incubation exists (HADFIELD, KAY, GILLETTE & LLOYD, 1972; CALVO, 1999). *Coralliophila meyerendorffii* and *Babelomurex babelis*, which show the same breeding behaviour (unattached capsules) than *Coralliophila abbreviata* and *Leptoconchus* lack a ventral pedal gland (RICHTER & LUQUE, in press). In *Coralliophila caribaea*, the presence of a filament fixing the egg-capsules to the foot might indicate to the contrary the existence of a ventral pedal gland, since in Neogastropods the formation of a stalk in the capsule is linked to a moulding and fixing process carried out by the ventral pedal gland (ANKEL, 1936). If brooding type in coralliophilids is related to the presence or absence of a pedal gland it might be a good systematic criteria, since the loss of a pedal gland is an evolutionary step. Whether more coralliophilid species exhibit the same breeding mechanism than *Coralliophila caribaea*, and whether this is linked to the existence of a ventral pedal gland should be find out. If, in fact, a ventral pedal gland exists, its presence should be regarded as a primitive character, and its absence as a secondary loss.

Brood care has been also reported in volutids (MARCHE-MARCHAD, 1968, 1977, 1980; PENCHASZADEH & DE MAHIEU, 1976; KNUDSEN, 1993) and buccinids (HUGHES, 1986), but in these groups females breed the egg-capsules in the ventral pedal gland. Therefore, within the frame of neogastropod phylogeny, brooding inside the pallial cavity could be considered as a synapomorphy of coralliophilids. However, as discussed later on, brooding can be only considered as a synapomorphy of a subgroup of coralliophilids, because its existence remains unknown in most species, and particularly in key species like *Coralliophila squamosa*, which, as suggested by RICHTER & LUQUE (in press) and supported by the present phylogenetic analysis, might represent a primitive coralliophilid with a primitive organisation of the reproductive system.

Protoconch and larval development

The protoconch of coralliophilids is unknown in most of species, because it is usually lacking or eroded in adult and even young specimens. In some genera, the protoconch of a single or a few species have been studied. Nevertheless, a protoconch with a multispiral larval shell with sinusigerous lip and strong knobbed spiral cords crossed by axial ribs has been considered to be diagnostic for coralliophilids (ROBERTSON, 1976; RICHTER & THORSON, 1975; SCHELTEMA & WILLIAMS, 1983; RIEDL, 2000). Most of recent species in which the protoconch is known presents such a type of larval shell (D'ATTILIO, 1972; RICHTER & THORSON, 1975; ROBERTSON, 1976, 1980; SCHELTEMA & WILLIAMS, 1983; TAVIANI & TAVIANI, 1986; LEAL, 1991; RIEDL, 2000; VEGA, VEGA & LUQUE, 2002), which indicates a plankto-

trophic development and appears in the fossil record at the Middle Eocene (LOZOUET & RENARD, 1998; RIEDL, 2000). However, D'ATTILIO (1972) and KOSUGE (1985 a, b; 1986 a, d; 1998) reveal a much wider diversity of protoconchs, that also include globose, paucispiral and smooth larval shells indicating a non-planktotrophic development.

Table 3 lists species whose protoconch has been described. Each protoconch with preserved microsculpture is classified morphologically according to the number of whorls and microsculpture and designated with a number. Correlation between number and protoconch morphology is as follow:

- 1) multispiral (more than 2 whorls) with 2 spiral cords and axial ribs.
- 2) multispiral (more than 2 whorls) with a single spiral thread
- 3) multispiral (more than 2 whorls) globose and smooth.
- 4) paucispiral (up to 2 whorls) with spiral cords and axial ribs.
- 5) paucispiral (up to 2 whorls) with faint spiral sculpture.
- 6) paucispiral (up to 2 whorls) with faint axial sculpture.
- 7) paucispiral (up to 2 whorls) globose and smooth.

Data on bathymetric range, geographic distribution and type of larval development are also indicated. In most species mode of development has not been directly observed and is here inferred from morphological characters of protoconch. Morphological types 1 and 2 correspond to planktotrophic, while type 7 to non-planktotrophic development. The modes of larval development that correspond to type 3, 4, 5 and 6 has still to be verified by studying the protoconch with SEM and culturing spawns until hatching of larvae.

The different types of protoconch suggests that it might be of taxonomic value in coralliophilids, at least at specific level. However, more information is needed in order to assess the value of protoconch morphology at supraspecific level. According to D'ATTILIO (1972), protoconch is not useful in defining genera, but might reflect zoogeographical boundaries. As shown in table 3, there is a relative high incidence of paucispiral smooth protoconchs in the Western Pacific when compared to the Atlantic basin, where at present no species with a paucispiral smooth protoconch has been described. In the Western Pacific 18% of the species (4 out of 22) bear paucispiral and smooth protoconch indicating non-planktotrophic development. These species belong to three genera (*Babelomurex*, *Hirtomurex* and *Mipus*), which also have planktotrophic species with multispiral axially and spirally ribbed protoconchs. Protoconch has also apparently ecological implications. A goodness of fit test reveals that the factor of number of whorls (paucispiral vs. multispiral) is significantly linked to depth range (deep sea vs. shallow waters vs deep sea-shallow waters) ($X^2 = 15.12$; $p < 0.001$; $df = 2$). Type of larval development also seems to depend on depth range ($X^2 = 52.6$; $p < 0.001$; $df = 2$), with non-planktotrophic development apparently restricted to deep sea localities (12%, 0% in shallow waters). It should be investigated whether the shift from planktotrophy to non-planktotrophy in Coralliophilidae is like in other caenogastropods an adaptative response to ecological factors or whether it is related to local historical fac-

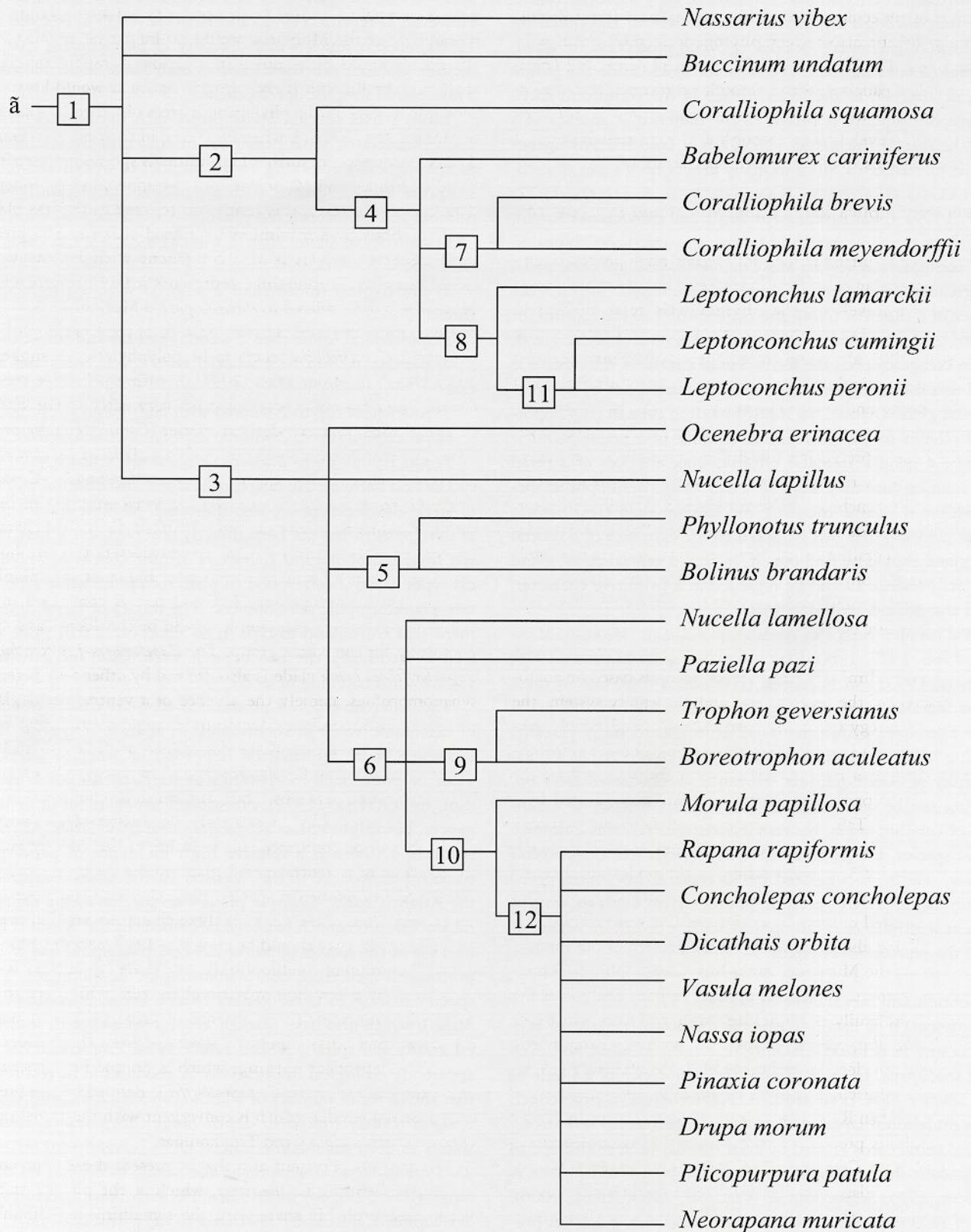


Figure 1. Strict consensus cladogram generated in the analysis.



tors (changes in sea level, water currents, temperature fluctuations during Late Pliocene- Pleistocene).

In spite of its ecological and biogeographical implications, protoconch might also reflect phylogenetic relationships in coralliophilids. The Western Pacific species of *Mipus* and *Hirtomurex* that have paucispiral and smooth protoconch and similar teleoconchs might have evolved from a common ancestor with planktotrophic development through a process that involves a transversal and subsequent allopatric speciation.

Phylogenetic implications of anatomical and reproductive characters

As pointed out in introduction, only recent phylogenetic analysis using molecular characters has been shown to be a good approach for unravelling the phylogenetic relationships of Coralliophilidae. HARASEWYCH *et al.* (1997) and OLIVERIO & MARIOTTINI (2001 a) demonstrated the close affinity between muricids and coralliophilids as suggested by their similarities in external anatomy and shell. The analysis of the latter authors, who compared sequences coding for 12S rDNA of five coralliophilid species representing five different coralliophilid genera and three muricids representing three subfamilies (Rapaninae, Muricinae and Ocenebrinae) also revealed the coralliophilids as a monophyletic clade within the Muricidae. The internal relationships of the coralliophilids, however, were only partly resolved. The different phylogenetic trees obtained only coincided in that the "spiny" group (*Babelomurex*, *Hirtomurex* and *Latiaxis*) was a monophyletic clade.

The present preliminary phylogenetic analysis based on anatomical characters of the reproductive and alimentary system, the reproductive strategy (sexuality, parental care) and larval development generates a strict consensus tree (Fig. 1) that reveals the Coralliophilidae as a monophyletic group characterised by the synapomorphy of protandry, assuming that, as suggested by a few evidences (see Tab. 2), *C. squamosa* and *Leptoconchus* species are protandric. The character state changes at each node are given in Appendix 3, corresponding to the nodes numbers on the cladogram in Fig. 1. Thus, the result supports the monophyly pointed out by the analysis of OLIVERIO & MARIOTTINI (2001 a), and also coincides with the pattern of the internal relationships of the Muricidae excluding Coralliophilidae obtained by these authors. Rapaninae appears in both analysis as the most derived subfamily of Muricidae, while an Ocenebrinae species, *Nucella lapillus*, represents together with the paraphyletic *Ocenebra erinacea* the less derived taxon of the Muricidae. *Phyllonotus trunculus*, a Muricinae species, is more derived than *Nucella lapillus* and less than Rapaninae. However, contrary to the phylogenetic hypothesis proposed by OLIVERIO & MARIOTTINI (2001 a), that holds that Coralliophilinae represents an evolutionary line within Muricidae, with the Rapaninae being a sister taxon of Coralliophilinae, the present analysis splits Coralliophilidae and Muricidae into two independent monophyletic clades. The monophyly of Muricidae is supported by the synapomorphies of presence of accessory boring organ (ABO), and presence of more or less developed right and left accessory salivary glands. The lat-

ter can be secondarily lost as occur in *Drupa* (WU, 1973; KOOL, 1993 a). However, if the key species *Coralliophila squamosa* would present an ABO and/or both accessory salivary glands, the monophyly of the Muricidae would no longer be sustained and the group would break down into various paraphyletic clades, while the coralliophilids excluding *C. squamosa* would keep their monophyly. One of the phylogenetic trees obtained by OLIVERIO & MARIOTTINI (2001 a), when including in their analysis four 12 S rDNA sequences of further four muricids species, also separates Coralliophilidae and Muricidae into two monophyletic independent clades. However, this result was rejected as the less plausible hypothesis by a maximum likelihood analysis. The present phylogenetic analysis is also congruent with HARASEWYCH (1984) in that Trophoninae represents a late offshoot of the Muricidae closely related to *Paziella pazi*, a Muricinae.

Concerning the internal relationships of the Coralliophilidae, the genus *Coralliophila* seems to be polyphyletic, as suggested by OLIVERIO & MARIOTTINI (2001 a), with a primitive species, *Coralliophila squamosa* branching off very early at the base of coralliophilids, and two derived species (*Coralliophila meyendorffii* and *C. brevis*) that appear grouped in a clade with *Leptoconchus* and *Babelomurex*. This clade of *Babelomurex*-*Leptoconchus*-*C. meyendorffii*-*C. brevis* is characterised by the synapomorphy of brood care in the mantle cavity, an often invoked diagnostic character for coralliophilids, and by other two characters that are homoplastic (absence of female gonopericardial duct and planktotrophic larval development). If brood care is confirmed in the primitive species *C. squamosa*, it should be considered as a synapomorphy for the whole group. The *Babelomurex*-*Leptoconchus*-*C. meyendorffii*-*C. brevis* clade is also defined by other four potential synapomorphies, namely the absence of a ventral pedal gland, the fusion of the salivary ducts into a single duct, a long vestibule and the reduction of the dorsal lobe of the capsule gland. All of them occur in *Babelomurex* and *C. meyendorffii* (RICHTER & LUQUE, in press; pers. obs.), but still has to be confirmed in *Leptoconchus* species. In *C. brevis* only the fusion of the salivary glands has to be confirmed. If the fusion of the salivary glands, the absence of a ventral pedal gland and a long vestibule are confirmed in *Leptoconchus* species, these characters turn out to be synapomorphies of the clade. If these characters are also present in *C. squamosa*, they should be considered as synapomorphies for the whole group of coralliophilids. The clade *Leptoconchus* is characterised by a few homoplastic characters which are shared with other muricids (i. e., absence of proximal sperm pouch) and by a small bursa copulatrix separated from the oviduct and with an independent opening, which is unique for *Leptoconchus*, while the clade *C. brevis*-*C. meyendorffii* is defined by the presence of a penial papilla, which is convergent with the penial papilla of *Buccinum undatum* and Trophoninae.

The analysis point out also that at present there is no autapomorphy defining *C. squamosa*, which at the present state of knowledge probably share with the remaining coralliophilids only a reproductive strategy characterised by a sex change from male to female (see above and Tab. 2), and this has still to be corroborated by histological methods and field or laboratory monitoring.



From the above it becomes evident that phylogenetic analysis based on anatomical and reproductive characters is useful as an alternative approach for the establishment of relationships within coralliophilids and among coralliophilids and muricids. Nevertheless, still much work has to be done in that sense. Further phylogenetic analyses including more species and genera, specially key species with primitive characters (i. e., *C. squamosa*), and more information on anatomical and biological characters, in particular on characters that have been revealed in the present study as synapomorphies or potential synapomorphies, are necessary.

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Appendix 1

Lists of characters and their states used for the phylogenetic analysis

Reproductive biology

0. Reproductive behaviour: 0= non-brooding; 1= brooding inside the pallial cavity.

Female reproductive system

1. Gonopericardial duct: 0= absent; 1= present.
2. Dorsal lobe of the capsule gland: 0= reduced; 1= well developed.
3. Anteroventral lobe of the capsule gland: 0= absent; 1= present.
4. Proximal sperm pouch (= seminal receptacle or sperm ingesting gland) between albumen gland and capsule gland: 0= absent; 1= present.
5. Posterior seminal receptacles: 0= absent; 1= connected to oviduct between albumen gland and sperm ingesting gland.
6. Seminal receptacle associated to albumen gland: 0= absent; 1= present.
7. Duct leading from the oviduct to the proximal sperm pouch: 0= absent; 1= lined by a ciliated epithelium; 2= lined by a smooth epithelium.
8. Vestibule: 0= vestibule short, does not extend appreciably beyond capsule gland; 1= vestibule long.
9. Bursa copulatrix: 0= continuous with capsule gland; 1= lateral diverticulum of anterior oviduct sharing a common genital pore with the oviduct 2= lateral diverticulum of anterior oviduct with an independent opening to the pallial cavity distinct from that of the oviduct

Male reproductive system

10. Gonopericardial duct: 0= absent; 1= reduced to a blind diverticulum; 2= present.
11. Prostata: 0= with proximal slit-like opening; 1= completely closed; 2= with a short muscular duct connecting pallial cavity with lumen.
12. Prostata: 0= without subepithelial gland cells; 1= with subepithelial gland cells.
13. Penis tip: 0= without papilla; 1= with papilla.
14. Vas deferens: 0= without subepithelial glandcells; 1= with subepithelial glandcells
15. Prostata: 0= with line of closure; 1= without line of closure.
16. Blind diverticulum from renal organ to sperm duct: 0= absent; 1= present.

Sexual strategy

17. Sexual strategy: 0= dioecia; 1= protandry or ESD.

Accessory structures for the performance of egg-capsules

18. Ventral pedal gland: 0= absent; 1= present.

Alimentary system

19. Ducts of salivary glands: 0= one pair separated; 1= ducts fusing anteriorly in a single duct.
20. Accessory salivary glands: 0= absent; 1= both reduced to very short straight tubes; 2= one pair more or less developed with equal or unequal length.

Foot

21. Accessory boring organ: 0= absent; 1= present.

Mantle

22. Anal gland: 0= absent; 1= present.

Operculum

23. Operculum: 0= present; 1= absent.

Developmental traits

24. Larval development: 0= planktotrophic; 1= non-planktotrophic.



Appendix 2

Data matrix used for the phylogenetic analysis

Data compiled from FRETTER (1941), GOHAR & SOLIMAN (1963), HARASEWYCH (1984), KOOL (1988, 1993 a, b), AMOR (1990); OEHLMANN (1994); DEMAINTENON (2001), RICHTER & LUQUE (in press) unknown or not comparable.

| | |
|---|---------------------------|
| <i>Nassarius vibex</i> (Say, 1822) | 01?110010102101110100000? |
| <i>Buccinum undatum</i> Linnaeus, 1758 | 01111002?1?211??001000001 |
| <i>Trophon geversianus</i> (Pallas, 1774) | 0011000001001100001021101 |
| <i>Boreotrophon aculeatus</i> (Watson, 1882) | 0011000000001100001021101 |
| <i>Morula papillosa</i> Schumacher, 1817 | 0??0110?00?11000001021100 |
| <i>Rapana rapiformis</i> (Born, 1778) | 0??1101?00?11000001021100 |
| <i>Concholepas concholepas</i> (Bruguère, 1789) | 0???101?00?11000001021100 |
| <i>Dicathais orbita</i> Gmelin, 1791 | 0??1101?00?11000001021100 |
| <i>Vasula melones</i> (Duclos, 1832) | 0??1101?00?11000001021100 |
| <i>Nassa iopas</i> H. & A. Adams, 1853 | 0??1101?00?11000001021100 |
| <i>Pinaxia coronata</i> H. & A. Adams, 1853 | 0??1101?00?11000001021100 |
| <i>Drupa morum</i> Röding, 1798 | 0??1101?00?11000001021100 |
| <i>Pliocypura patula</i> (Linnaeus, 1758) | 0??1101200?11000001021100 |
| <i>Neorapana muricata</i> (Broderip, 1832) | 0???101?00?11000001021100 |
| <i>Phyllonotus trunculus</i> (Linnaeus, 1758) | 0111100??10000000010?1101 |
| <i>Bolinus brandaris</i> (Linnaeus, 1758) | 0111100??10000000010?1101 |
| <i>Ocenebra erinacea</i> (Linnaeus, 1758) | 0111100201101000001021101 |
| <i>Nucella lamellosa</i> (Gmelin, 1791) | 0011100?01001000001021101 |
| <i>Nucella lapillus</i> (Linnaeus, 1758) | 0111100201001000001021101 |
| <i>Babelomurex cariniferus</i> (Sowerby, 1834) | 100010011100100001011?100 |
| <i>Coralliophila brevis</i> (Blainville, 1832) | 10?0100?11??1100010???10? |
| <i>Coralliophila meyendorffii</i> (Calcara, 1845) | 100010011100110001010?100 |
| <i>Leptoconchus cumingii</i> Deshayes, 1863 | 10??0000?201?00001??00010 |
| <i>Leptoconchus peronii</i> (Lamarck, 1818) | 10??0000?201?00001??00010 |
| <i>Leptoconchus lamarckii</i> (Deshayes, 1863) | 10??0000?201?00001??00000 |
| <i>Coralliophila squamosa</i> (Bivona, 1838) | ?1?1100??100100001?????0? |
| <i>Paziella pazi</i> (Crosse, 1869) | 0011100?00001000001021101 |

Appendix 3

Character state changes

Changes in characters are based on the strict consensus tree of Figure 1. The node numbers correspond to those given in the same figure. Arrows indicate the direction of change. Synapomorphies are indicated with bold letters and potential synapomorphies with * (for explanation see text).

node 1 → node 2: **character 17: 0 → 1.**

node 1 → node 3: **character 7: 1/2 → 2, character 20: 0 → 2, character 21: 0 → 1**

node 2 → node 4: **character 0: 0/1 → 1, character 1: 1 → 0, character 2*: 1 → 0, character 3: 1 → 0, character 8*: 0/1 → 0, character 18*: 0/1 → 0, character 19*: 0/1 → 0.**

node 3 → node 5: **character 12: 1 → 0.**

node 3 → node 6: **character 1: 1 → 0, character 9: 1 → 0/1.**

node 4 → node 7: **character 13: 0 → 1, character 22: 0/1 → 1.**

node 4 → node 8: **character 4: 1 → 0, character 7: 1 → 0, character 9: 1 → 2, character 11: 0 → 1, character 22: 0/1 → 0.**

node 6 → node 10: **character 9: 0/1 → 0, character 11: 0 → 1.**

node 6 → node 9: **character 3: 1 → 0, character 7: 2 → 0, character 13: 0 → 1.**

node 8 → node 11: **character 23: 0 → 1.**

node 10 → node 12: **character 6: 0 → 1.**