Anatomy and histology of *Corambe lucea* Marcus, 1959 (Gastropoda, Nudibranchia, Doridoidea), with a discussion of the systematic position of Corambidae

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Abstract

The phylogenetic position of Corambidae has been subject to much speculation. Most of the confusion has arisen from insufficient anatomical knowledge and from interpretations which have not followed the rules of Hennigian phylogenetic systematics. In this study, as a model system, the poorly known Chilean species *Corambe lucea* Marcus, 1959 is redescribed in detail: digestive, reproductive, central nervous, circulatory, and excretory systems are examined anatomically and histologically. New biological data are also given. After critical comparison with congeners, *C. lucea* is confirmed to be a valid species. Major organ systems of *C. lucea* are discussed comparatively and used to resolve phylogenetic relationships. Gill structure and circulatory system of the Corambidae are homologous to that of the Anthobranchia bauplan but not to the secondary gills and circulatory system of the Phyllidiidae. The similar lateral position of respiratory organs and a posteroventral anus in some Corambidae and Phyllidiidae is clearly due to convergence; the two groups are true doridoidean nudibranchs but there is no indication for a sistergroup relationship. Corambids are shown to belong to the monophyletic group Suctoria which is characterized by the unique and complex autapomorphies "possession of a dorsal buccal pump" and "possession of a large first lateral tooth with a long, denticulated hook".

Key words: Nudibranchia, Corambidae, *Corambe lucea*, morphology, phylogeny

Introduction

Members of the nudibranch family Corambidae Bergh, 1871 have always attracted taxonomists' interest. This is primarily due to their aberrant morphology relative to other dorid nudibranchs, i.e. their flattish shape, posteroventral anus and gills, notal cuticle, lobed digestive gland, dorsoventral septa and peculiar circulatory system. The phylogenetic position of Corambidae has been highly controversial. On one hand, close relationship to certain members of the enigmatic family Phyllidiidae was proposed due to the similar position of anus and gills (Bergh, 1871; Tardy, 1970; Minichev, 1970; Minichev & Starobogatov, 1979, 1984). Assuming an evolutionary shift of the anus and gills from an ancestral frontal to a right side position in Doridoxidae, to a ventral and terminal position in Corambidae and Phyllidiidae, and finally to the dorsal side in other Doridoidea, Baranetz &

Minichev (1994; 1995) suggested a very basal phylogenetic position of Corambidae: they renewed an earlier proposal of an order Corambida Minichev & Starobogatov, 1979, separate from other Doridoidea plus Bathydoridoidea. These analyses, however, showed hypothetical evolutionary stages of single organ systems that do not necessarily reflect phylogenetic clades.

On the other hand, corambids were related to phanerobranch Doridoidea (Valdés & Gosliner, 2000), usually to the suctorian families Onchidorididae and Goniodorididae (e.g. Fischer, 1891; MacFarland & O'Donoghue, 1929; Marcus, 1959). In their cladogram, Millen & Nybakken (1991) regarded the Corambidae as a basal offshoot of the Suctoria. Main reasons were the synapomorphies "possession of a dorsal sucking crop and a reduced number of similarly differentiated radular teeth". However, Millen & Nybakken (1991) pointed out difficulties in explaining the separate condition of the cere-

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bral and pleural ganglia in corambids. Separate cerebral and pleural ganglia are present in many other opistho-branchs (e.g. Cephalaspidea, Anaspidea) but only in a few nudibranchs (i.e. Bathydoridoidea, *Actinocyclus*, *Gymnodoris*, Vayssiereidae). Most other nudibranchs possess fused pleural and cerebral ganglia. Martynov (1994b [in Russian], 1995 [English translation]) doubt-ed the primitive nature of corambids and regarded them as progenetic derivatives of onchidorid ancestors simi-lar to the genus *Adalaria* Bergh, 1878. Valdés & Bouchet (1998) presented a cladogram of corambids with *Adalaria* as the single outgroup. Of ten characters used, nine were external or radular features.

Despite the phylogenetic interest in the group, there are few studies on corambid anatomy and histology. The most detailed ones are still those of Fischer (1891) and MacFarland & O'Donoghue (1929), describing *Coram-be testudinaria* Fischer, 1889 and *Corambe pacifica* MacFarland & O'Donoghue, 1929. The original de-scription of *Corambe lucea* Marcus, 1959 lacks infor-mation about several taxonomically and phylogenetical-ly important organs like genital, circulatory, excretory, nervous, and posterior portions of the digestive system. This Chilean species appeared to be very similar to the better known Californian *Corambe pacifica* (Marcus, 1959; Swennen & Dekker, 1995). In the same way, sev-eral other Chilean nudibranch species have recently been found to be closely related or even conspecific with temperate northeastern Pacific congeners (Schrödl, 1996, 1997; Millen & Schrödl, in review).

In this study, *C. lucea* is redescribed anatomically and histologically, and critically compared with con-geners. Main organ systems are discussed comparative-ly and used to elucidate the systematic position of the Corambidae.

Material and methods

Abbreviations used for institutions: Zoologische Staatssamm-lung München, Germany (ZSM). The Natural History Muse-um, London, United Kingdom (BMNH). Zoologisk Museum, Copenhagen, Denmark (ZMUC).

Corambe lucea: Caleta Buena (22°25′S, 70°15′W): 2 spec-imens (one dissected), March 17, 1994, 7 m, on *Macrocystis pyrifera* (L.) covered with *Membranipora isabelleana* D'Orbigny, ZSM No. 1912. Bahía de Coliumo (36°32′S, 72°57′W): 4 specimens (two dissected), 31 January 1994, 0–5 m, on *Macrocystis pyrifera*, ZSM No. 1913. Faro Corona (41°50′S, 73°52′W): about 20 specimens (seven dissected, three serially sectioned), 24 December 1994, 0–3 m, on *Macrocystis pyrifera* covered with *Membranipora isabel-leana*. Bahía de Ancud (41°52′S, 73°55′W): 2 specimens, De-cember 25, 1994, 0–4 m, on *Macrocystis pyrifera*.

Methods: The specimens were observed *in situ* and collect-ed using SCUBA. After feeding observations in aquaria they were narcotized with a 10% MgCl$_2$ solution and preserved in 70% ethanol. Ten specimens were dissected. Two adults and one juvenile were embedded in hydroxyethylmethacrylate (Kulzer) for serial sectioning. The 2.5 µm sections were stained with toluidine-blue and microscopically examined. Digestive, reproductive, central nervous, circulatory and ex-cretory systems were reconstructed. Histological investiga-tions on cellular level were done as detailed as possible. The radulae and, after critical point drying, the relevant soft parts were gold coated and examined using a Philips XL 20 Scan-ning Electron Microscope.

Other material: For comparison, specimens of similar *Corambe* species have been examined. *Corambe pacifica* Mac-Farland & O'Donoghue, 1929: Mission Bay, San Diego, U.S.A., 3 specimens, 3 July 1996, coll. by S. Millen and W. Farmer, on stranded kelp. All 67 "paratypes of *Corambe pacifi-ca*" by original designation, BMNH, collected at Vancouver Is-land, Canada, probably O'Donoghue det., in fact are *Corambel-la steinbergae* Lance, 1962. *Corambe sargassicola* det. Bergh, Sargasso Sea, 16 specimens (non-type material), ZMUC, are identified as being *Corambe testudinaria* Fischer, 1889.

Abbreviations used in the figures

am	ampulla
ao	aorta
at	atrium
agv	afferent gill vessel
av	afferent vessel
b	buccal pump with median muscle stripe
bc	bursa copulatrix
bg	blood gland
cag	capsule gland
cg	cerebral ganglion
dg	digestive gland lobes (covered by gonad tissue)
dgc	digestive gland cavity
dm	dorsoventral muscle-bundles
e	oesophagus
egv	efferent gill vessel
ev	efferent vessel
fg	female gland mass
fs	foot sinus
g	gill
go	gonad
hd	hermaphroditic duct
in	proximal intestine
ov	proximal oviduct
p	pedal ganglion
pe	pericardium
phd	postampullar hermaphroditic duct
pl	pleural ganglion
pp	penial papilla
ps	penial sheath
rm	retractor muscle
sl	sinus lateralis
sr	sperm receptacle
v	vagina
va	vaginal duct
var	visceral artery

vd   prostatic vas deferens
ve   ventricle
vv   visceral vessel

Family CORAMBIDAE Bergh, 1871

Genus *Corambe* Bergh, 1869

Corambe lucea Marcus, 1959

Corambe lucea Marcus, 1959: 61–62, figs. 139–143; Millen & Nybakken 1991: 213; Valdés & Bouchet 1998: 15–20.

    Quasicorambe (Gulbinia) lucea Martynov 1994a: 3–15; 1994b: 36–43; 1995: 59–67.

    Neocorambe lucea Swennen & Dekker 1995: 104–105; Schrödl 1996: 29, pl. 5, fig. 28; 1997: 39–42.

External morphology (Figs. 1A,B,C,D)

Living specimens 3–10 mm in length, 1.5–6 mm in width, up to 2 mm in height (see Schrödl 1996: pl. 5, fig. 28). Largest preserved specimen with 9 mm length. Body flattened, completely covered dorsally by over-hanging, wide notum (Fig. 1A). Notum deeply notched posteromedially (Fig. 1B). Notum nearly smooth, bearing very small tubercles (Fig. 1D), covered by cuticle. Rhinophoral sheaths smooth, slightly elevated. Rhinophores completely retracted in preserved specimens. Solid, digitiform rhinophore axis anteriorly fused with two envelope-like sheaths. Head bearing oral veil with anterior corners prolonged into short oral tentacles (Fig. 1B). Anterior foot border not notched, curved backwards medially. Posterolateral row of 9 to 14 contractible gills on each side, between notum and foot.
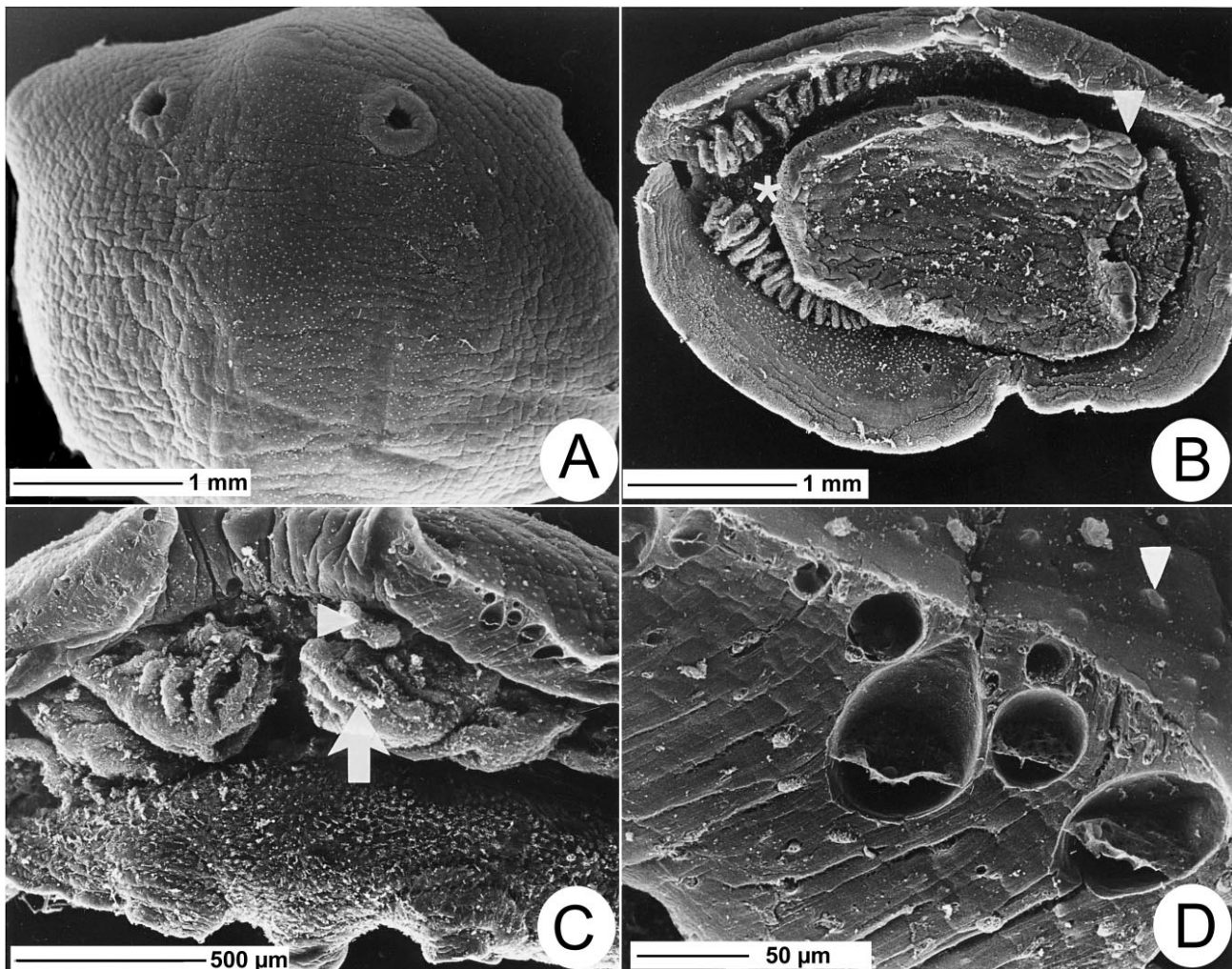

Fig. 1. A–D. *Corambe lucea*, SEM micrographs. **A.** Dorsal view; scale bar = 1 mm. **B.** Ventral view; posterior parts of the foot removed. Anus position indicated by an asterisk, genital openings with an arrowhead; scale bar = 1 mm. **C.** View on the posterior end of the body; posterior parts of the notal lobes removed. Note the large lateral gills (arrow) and a small "central" gill (arrowhead); scale bar = 0.5 mm. **D.** Section through the notum; note the tiny notal tubercles (arrowhead) and the large cells aggregated under the notum surface; scale bar = 50 μm.

Gills feather-like with broad base. Up to 8 sloping transversal leaflets inserting on both sides of central axis. Arrangement of leaflets alternating, but sometimes irregular (Fig. 1C). Gill size decreasing from large posterior to very small anterior ones in both lateral rows. Large specimens with up to three additional ("central") gills situated more postero-medially (Fig. 1C), much smaller than neighbouring lateral ones, but agreeing in general shape. Medially, always a gap present between the gill rows. Anus and nephroproct in medial, posteroventral position between notum and foot. Genital openings on right side at level of rhinophore.

Anatomy

Digestive system (Figs. 2, 3A,B). Oral tube short with a pair of bulbous oral glands opening laterally. Labial disc, pharynx and buccal pump lined with smooth cuticle. Large, rounded buccal pump sitting dorsally on the pharynx, with a median stripe of longitudinal muscles (Fig. 2). Radular sac narrow, projecting. Radular formula 35–47 × 5–6.1.0.1.5–6. Large, first lateral teeth bearing a long hook with 5-8 inner denticles (Figs. 3A,B). Outer side of first laterals with long basal projection. Smaller marginal teeth with rectangular base and slightly elongate hook. One pair of coiled, tube-like salivary glands. Wide oesophagus rising posteroventrally to buccal pump and opening ventrally into the wide central cavity of the fused stomach/digestive gland lumen; no distinct stomach detectable. Digestive gland compact, peripherally divided into two lateral pairs of lobes and one posterior lobe by two lateral pairs of dorsoventral muscle bundles (Fig. 2). Third pair of muscles anteriorly between pharynx and rhinophores. Anterior right digestive gland lobe usually displaced or strongly reduced by female gland mass in larger specimens, anterior left lobe by an extensive, compact gonad. Proximal intestine wide, muscular, longitudinally folded. Intestine arising dorsally from stomach/digestive gland cavity, running anteriorly along the digestive gland surface. Curving backwards, the distal intestine narrows towards the posterior anus

Reproductive system (Fig. 4). Gonad covering digestive gland dorsally and laterally in a thick layer and filling out spaces between digestive gland lobes; anteriorly, often displacing first left digestive gland lobe. Ampulla wide and spherical. Hermaphroditic duct half surrounding ampulla before dividing into oviduct and vas defer-
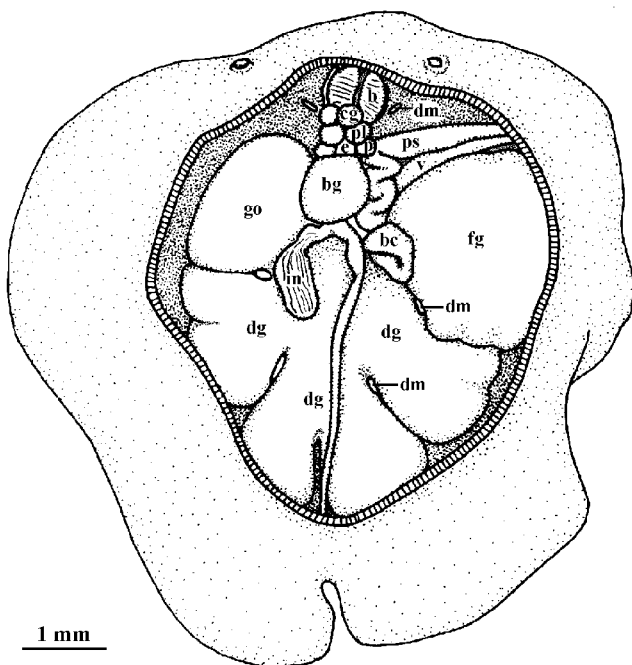

Fig. 2. *Corambe lucea*, semischematic outline of the internal organisation of a large specimen; notum, salivary glands, circulatory and excretory organs removed; scale bar = 1 mm.
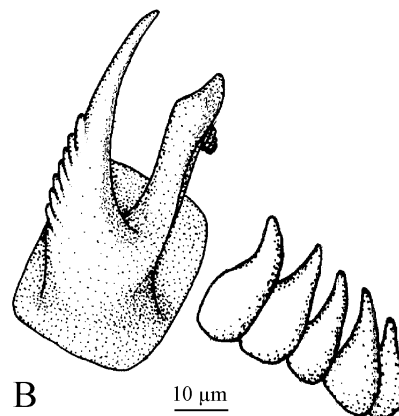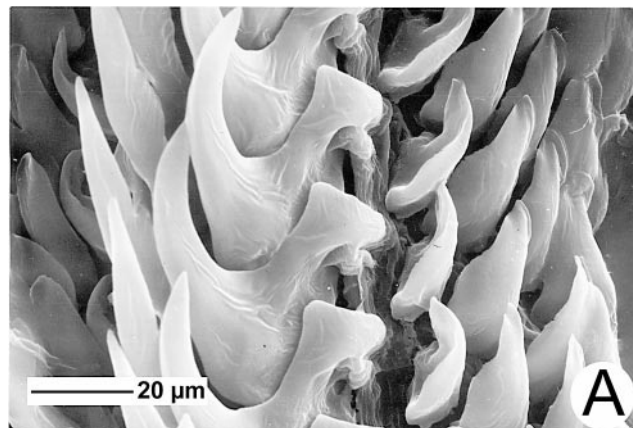

Fig. 3. **A–B**. *Corambe lucea*, radula. **A.** SEM micrograph. Large, first lateral tooth and reduced marginal teeth; scale bar = 20 μm. **B.** Drawing of the first lateral (note the inner denticles) and marginal teeth; scale bar = 20 μm.
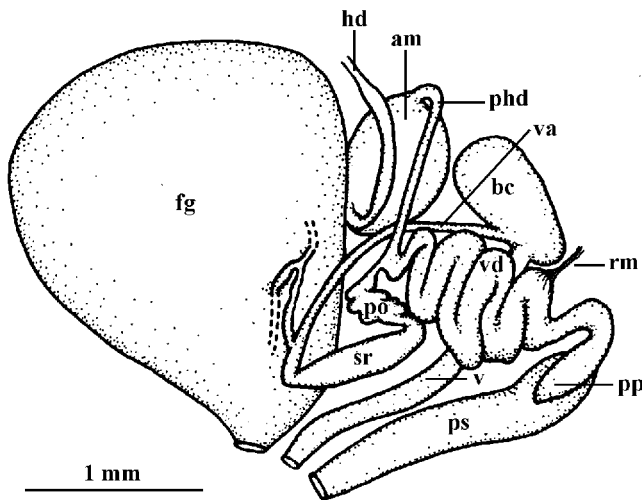
Fig. 4. *Corambe lucea*, genital system; scale bar = 1 mm.

Fig. 5. *Corambe lucea*, circulatory system, schematic outline.

ens. Proximal vas deferens soon becoming thick, forming several prostatic loops. Strong retractor muscle inserting on thinner distal, muscular vas deferens. Large conical penial papilla armed with cuticle. Penis usually retracted into long, wide penial sheath.

After some loops, proximal oviduct widening into serially arranged sperm vesicle; more distally division into oviduct entering capsule and mucous glands with two separate branches, and into long, thin vaginal duct. The latter entering into large ovate, serially arranged bursa copulatrix subterminally. Terminally, bursa giving rise to long and wide, longitudinally folded vagina.

Central nervous system (CNS). Virtually identical to that of *C. pacifica* described by MacFarland & O'Donoghue (1929: pls. 2,3, figs. 8–10). Cerebral ganglia connected with short commissure. Rhinophore nerves with small ganglion at their base. Optic ganglia attached to cerebral ganglia. Optic nerves long. Pleural and pedal ganglia separate from cerebral ganglia, with very short connectives. Statocyst containing approximately 10 to 15 otoconia, nestling between pleural and pedal ganglia. Cerebropedal and pleuropedal connectives very short. Visceral loop short; with small visceral ganglion close to right pleural ganglion. Buccal ganglia, bearing two separate buccal nerves, close together.

Circulatory sytem (Figs. 2, 5). Muscular ventricle with posterior atrium lying in a spacious pericardium. Aorta dividing into visceral artery and branching artery running cranially. One main branch entering into blood gland, which is a flat, rounded lobe above oesophagus, slightly posterior to CNS (Fig. 2). Wide visceral vessel
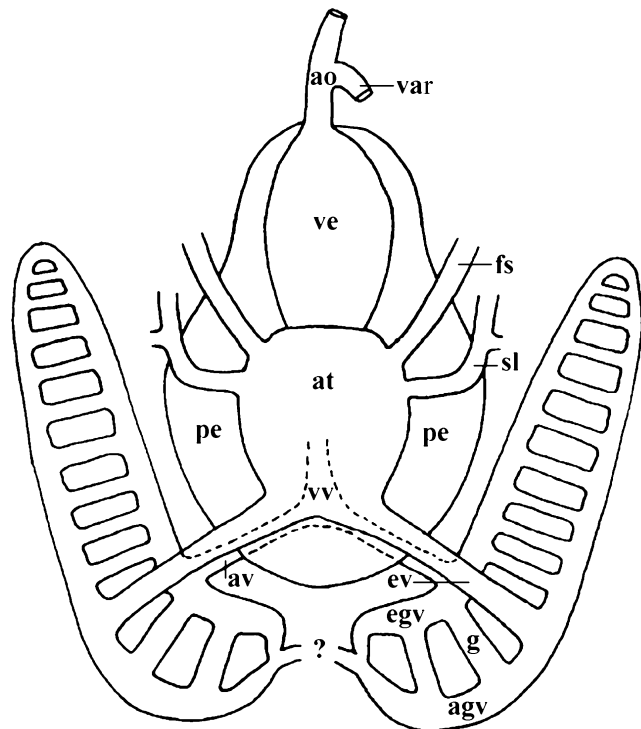
situated mediodorsally on digestive gland. Two afferent gill vessels running posterolaterally, dividing into two branches: 1) wide afferent vessel entering into largest, most posteriorly situated lateral gills with a narrow vessel continuing beyond insertion of central gill. 2) main afferent gill vessel curving cranially and inserting into each of the more anterior lateral gills with short branches. At bases of gills, a pair of efferent vessels present, collecting hemolymph from anterior lateral gills, joining efferent vessels from the "central" and posterior lateral gills. The two efferent gill vessels curving cranially, opening terminally into the atrium. Hemolymph from mantle collected on each side of visceral cavity within wide lateral sinus. Both lateral sinuses with connecting duct entering into atrium laterally. Anteriorly, pair of pedal sinus leading into atrium.

Gill glands. Spherical gill glands situated at bases of posterior, large lateral gills but absent in more anteriorly lying, smaller lateral gills. Small "central" gills apparently also with corresponding gill glands. Two small specimens of *C. lucea* (3 mm length) without small "central" gills and corresponding gill glands.

Pericardium and excretory sytem. Pyriform syrinx rising from the right ventral side of the pericardium. Reno-pericardial duct long and narrow, first running

caudally, then curving and entering the kidney. Kidney forming elongated, blind sac anterior to junction with reno-pericardial duct. Posteriorly, kidney wide, completely enveloping proximal reno-pericardial duct as a strongly folded tube. Ureter short, opening close to anus.

Histology

Digestive system (Figs. 6A,B). Oral glands flocculent, multicellular (Fig. 6A). Cell limits not always detectable. In between areas with dark violet granules, areas containing purple staining vesicles and unstained areas, possibly vacuoles present. Oral glands clearly annexed with oral tube but no discrete efferent duct detect-

ed. Labial disc and pharynx with buccal pump, lined with smooth cuticle. Salivary glands with large, circularly arranged, dark violet staining cells with non-staining vacuoles. Oesophageal epithelium thin, without specialized vacuolated cells. Stomach fused with wide central cavity of the digestive gland (Fig. 6B); only remains of ciliated stomach epithelium detectable. Digestive gland cells glandular, lacking cilia. No caecum detected. Intestinal cells cuboidal, glandular, ciliated. Intestine with longitudinal folds but without typhlosole. Intestine covered by muscular layers, especially the proximal portion.

Genital system (Figs. 6B, 7A,B). Gonads composed of separate male and female follicles (Fig. 6B), closely
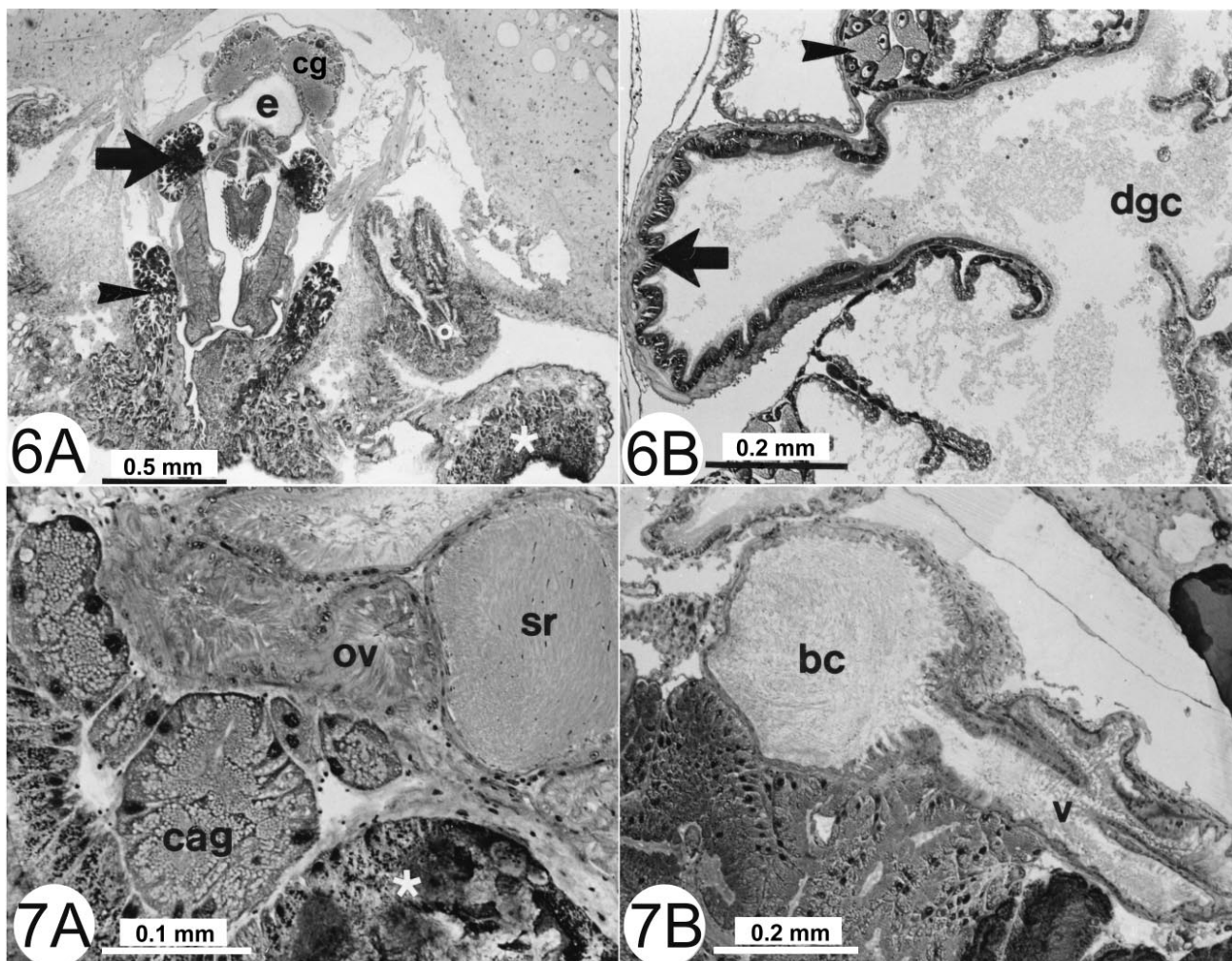

Fig. 6. **A–B.** *Corambe lucea,* histology of the digestive system. **A.** Section through the anterior part. Note the cerebral ganglia (cg) above the thin-walled oesophagus (e), the oral glands (arrowhead), and the salivary glands (arrow). Foot glands (asterisk) and distal genital ducts (circle) are also visible; scale bar = 0.5 mm. **B.** Section through the distal part, showing the fused stomach and digestive gland cavity (dgc), the ciliated intestinal wall covered by muscle layers (arrow), and the female gonad (arrowhead); scale bar = 0.2 mm
Fig. 7. **A–B.** Female genitals of *Corambe lucea.* **A.** Proximal oviduct (ov), sperm receptacle (sr); capsule gland (cag), and mucous gland (asterisk); scale bar = 0.1 mm. **B.** Bursa copulatrix (bc) and proximal vagina (v); scale bar = 0.2 mm.
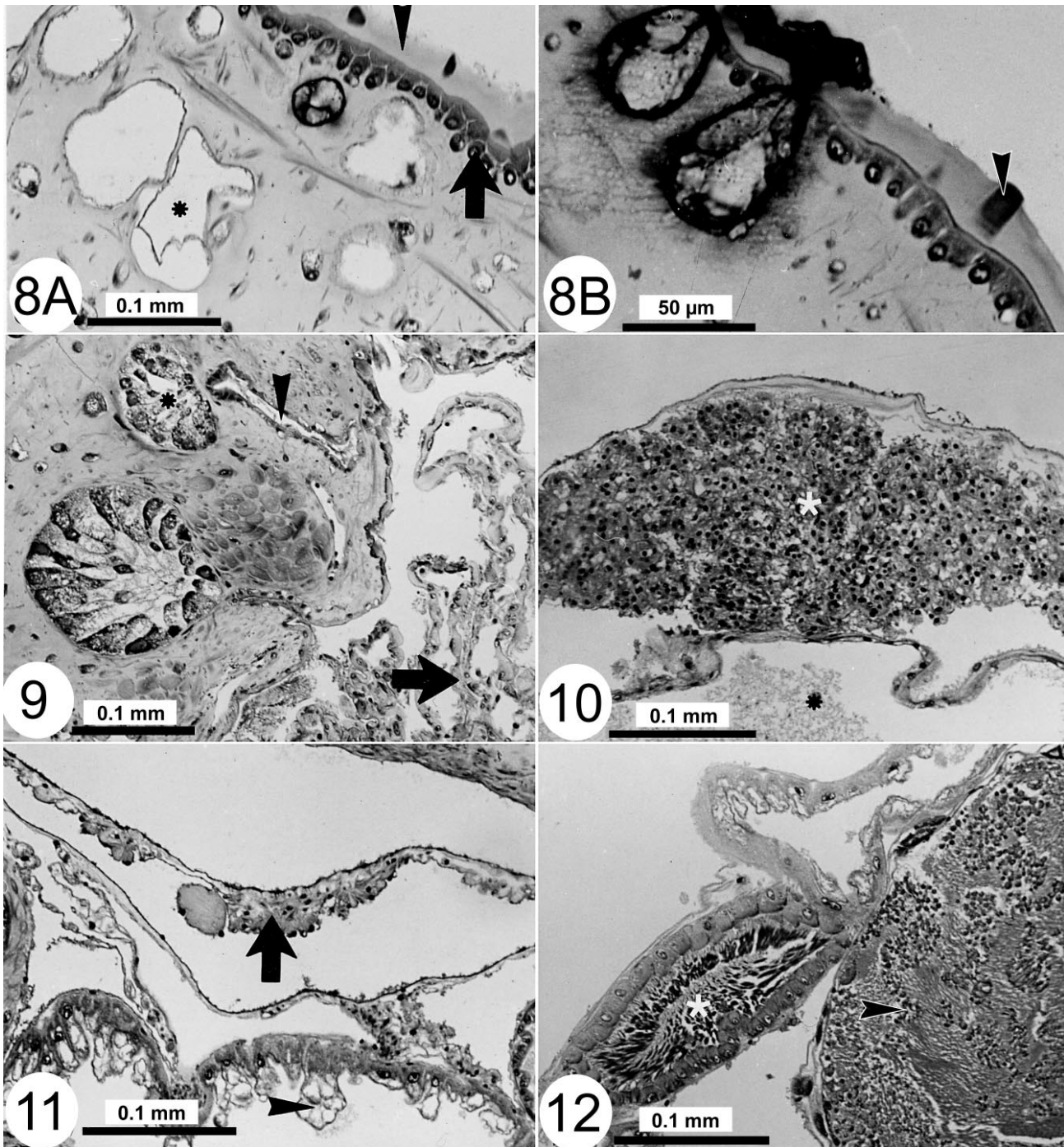
Fig. 8. A–B. Mantle histology of *Corambe lucea*. **A.** Overview; note the cuticle (arrowhead), glandular epidermal cells (arrow), and large, vacuolized mantle cells (asterisk); scale bar = 0.1 mm. **B.** Detail showing multicellular, subepidermal glands opening onto the notum surface and pegs within the cuticle (arrowhead); scale bar = 50 μm.

Fig. 9. *Corambe lucea*, gills and spherical, multicellular gill glands. Gill gland marked by an asterisk, gill gland duct by an arrowhead and gill epithelium by an arrow; scale bar = 0.1 mm.

Fig. 10. *Corambe lucea*, blood gland (white asterisk) and oesophagus (black asterisk); scale bar = 0.1 mm.

Fig. 11. *Corambe lucea*, pericardial glands (arrow) and kidney (arrowhead); scale bar = 0.1 mm.

Fig. 12. *Corambe lucea*, heavily ciliated syrinx (asterisk) and male gonad (arrowhead); scale bar = 0.1 mm.

attached to one another. Oogonia with large nuclei. Hermaphroditic duct thin-walled, ciliated. Ampulla thin-walled, filled with autosperm. Cilia not visible. Postampullary hermaphroditic duct ciliated. Muscular, ciliated proximal vas deferens widening into pink-staining prostate. Prostate cells large, cuboidal, glandular, without cilia. Distal vas deferens ciliated and covered by muscular layer. Penial papilla with cuticle. Penial sheath densely ciliated. Proximal oviduct folded, epithelium ciliated (Fig. 7A). Oviduct containing a few sperms not clearly attached to walls. Sperm vesicle thin-walled, without muscular layers; filled with sperm, many of them loosely attached to ciliated walls. Capsule gland comprised of large cells containing weakly blue staining vesicles. Large mucus gland cells densely filled with purple staining vesicles and granules indicating presence of mucopolysaccharides. Bursa formed by cuboidal glandular cells, lacking cilia (Fig. 7B). Bursa filled with light-bluish, fibrous mass containing sperm not orientated to the wall. Vagina epithelium heavily ciliated, without further glands.

Mantle (Figs. 8A,B). Notum covered dorsally by weakly staining cuticular layer. Ventrally, cuticle limited to periphery of mantle rim. Blue staining pegs within cuticle. Notal epithelium with cuboidal, blue staining glandular cells with basal nuclei. Specialized vacuolated cells not present. Dorsally, subepithelial, multicellular glands with large vacuoles in their cells; violet staining secretion reaching notum surface by short ducts. Thick layer of mantle connective tissue containing scattered fibres and nuclei. Spicules absent. Large, vacuolated cells concentrated under notum surface.

Foot (Fig. 6A). Prismatic epithelium, ciliated. Subepithelial follicular glands concentrated in anterior foot portion. Similar, violet staining multicellular glands additionally situated along foot rim.

Gills and annexed organs (Fig. 9). Gills with flat, ciliated epithelium. Gill leaflets with a few delicate trabeculae. Globular gill glands consisting of several large prismatic, violet staining cells. Each gland complex with narrow excretory duct of varying length opening at bases of gills. Retractor muscle fibres inserting into each gill.

Blood gland (Fig. 10). Aggregation of small, bluish staining cells with large, dark blue staining nuclei. No epithelium surrounding this organ detected.

Pericardial glands (Fig. 11). Anterodorsally, pericardium forming folds with irregularly shaped cells with inconspicuous, bluish staining properties, and unknown function.

Excretory system (Figs. 11, 12). Syrinx epithelium cuboidal, very heavily ciliated. Kidney cells irregularly shaped, highly vacuolized.

Biology

Corambe lucea was found at 0–7 m depth on *Macrocystis pyrifera*, usually on floating fronds covered with colonies of the bryozoan *Membranipora isabelleana* on which *C. lucea* was observed to feed *in situ* and in aquaria.

Adults of *C. lucea* as well as egg masses were found to occur at the Chilean coast during the summer months December to March. The egg masses are ribbons forming two to three spirals with a total diameter up to 5 mm. The transparent egg capsules contain a single white egg each. Preserved egg capsules measure 100 µm, preserved eggs 80–90 µm in diameter.

Geographic distribution (Fig. 13)

Corambe lucea was reported to occur from Caleta Buena (22°25'S, 70°15'W), northern Chile (Schrödl, 1997) to Golfo Corcovado (42°46'50"S, 73°12'10"W),

Fig. 13. Geographic distribution of *Corambe lucea.*

southern Chile (Marcus, 1959). A complete list of collecting localities was given by Schrödl (1996).

Discussion

Taxonomy

All corambid specimens from Chile examined during this and previous studies (Schrödl, 1996, 1997) agree with the external original description of *Corambe lucea* Marcus, 1959 collected at Chiloé Island, southern Chile (Marcus, 1959). Re-arranging the family Corambidae independently (Martynov, 1994a; Swennen & Dekker, 1995), *C. lucea* was placed into the new genera *Quasicorambe* (*Gulbinia*) Martynov, 1994, and *Neocorambe* Swennen & Dekker, 1995, respectively. These two corambid classifications were contradictory, resulted in an inflated amount of categories and synonymies, and were not based on phylogenetic analysis. An alternative classification with only three valid genera was proposed in a family revision by Valdés & Bouchet (1998). The new monotypic genus *Echinocorambe* Valdés & Bouchet, 1998 was considered to be the first corambid offshoot. Downgrading Martynov's subfamilies Loyinae and Corambinae to generic rank, the genus *Loy* Martynov, 1994 includes *Proloy* Martynov, 1994 and *Psammodoris* Martynov, 1994, while its direct sister group *Corambe* Bergh, 1869 contains *C. lucea* and the bulk of other higher derived corambid species (Valdés & Bouchet, 1998). This classification was based on a cladogram which on one hand seems reliable due to a single tree with high consistency index (0.88) obtained by parsimony analysis (see Valdés & Bouchet, 1998). It also reflects some general trends in corambid evolution suggested by Millen & Nybakken (1991) and Martynov (1994a, b, 1995), i.e. the ventral shift and special differentiation of gills, the loss of spicules, the special differentiation of rhinophores, and, considering the plesiomorphic *Echinocorambe*, the loss of rhachidian radular teeth within the family. On the other hand, the cladogram may be unstable for the following reasons: 1) of only ten characters selected, nine are external or radular ones; internal features other than the presence or absence of spicules were not considered. 2) character states were rooted using a single genus, the onchidorid *Adalaria*, despite the still doubtful systematic position of the Corambidae. 3) some characters need critical reconsideration, i.e. the gill shape (character No. 2) of *Echinocorambe* differs from both plume-like and plate-like gills of other corambids. The second lateral teeth (character 8) of *Loy* and *Proloy* differ considerably from the first ones (Martynov, 1994a) and may be equally regarded as marginal teeth. In particular, the secondary nature (Martynov, 1994b, 1995) of the fusion of the

notal notch (character 5) in *Loy* (wrongly referred to as "*Proloy*") must be seriously doubted if considering the dorsal position of anus and gills in *Loy* (see below). 4) character states of several taxa were confused in the data matrix; i.e. *Echinocorambe* was described to lack spicules while being coded to possess spicules (Valdés & Bouchet, 1998: table 2). *Loy* and *Gulbinia* were coded to have gills in a ventral position (over the anus). However, *Loy* was explicitly described to have dorsal anus and gills by Martynov (1994a: fig. 1A-C; 1994b, 1995); *Corambe lucea*, one of the species assigned to *Gulbinia*, has gills on each side but not over the anus (Marcus, 1959; this study). Therefore, in the present study we prefer to use original generic names for corambids to avoid further confusion.

Corambe lucea externally resembles the European *C. testudinaria* Fischer, 1889, the northeastern Pacific *C. pacifica* MacFarland & O'Donoghue, 1929, and the Brasilian *C. evelinae* Marcus, 1958, with a notal notch and many feather-like gills in two lateroventral rows. The Atlantic *Corambe sargassicola* Bergh, 1871 mentioned by Bergh (1892) to have feather-like gills in reality has broad plate-like gills (Bergh, 1871; Swennen & Dekker, 1995), and the notal notch originally reported from the holotype by Bergh (1871) was regarded to be an artifact by Swennen & Dekker (1995).

Corambe testudinaria was described to have fused cerebropleural ganglia (Fischer, 1891; García *et al.*, 1990) and clearly differs from *C. lucea* which has separate cerebral and pleural ganglia (this study). This unusual separate condition was also mentioned for *C. pacifica* by MacFarland & O'Donoghue (1929). Marcus (1959) distinguished *C. lucea* from *C. pacifica* by gill leaflets inserting alternately on a central axis whereas these are described to be opposing in *C. pacifica*. However, the original drawing of *C. pacifica* shows several gills with partly irregular or alternate leaflets (MacFarland & O'Donoghue, 1929: pl. 1, fig. 4). Since it is also difficult to define the exact insertion of leaflets in the broad and mostly sloping insertion area of *C. lucea*, the taxonomical value of this character must be doubted. However, the gills of *C. pacifica* with their more slender, feather-like shape with a small base (MacFarland & O'Donoghue, 1929; this study), clearly differ from those of *C. lucea* which possesses more stout gills with a broad base (Marcus, 1959; this study). *Corambe pacifica* posteriorly has large gills in a more or less continuous band. In contrast, *C. lucea* posteriorly has a considerable gap between both gill rows (Fig. 1B); at both sides of this gap, larger specimens usually have one or two small "central" gills which do not occur in *C. pacifica* (see MacFarland & O'Donoghue, 1929). Small "central" gills were also absent in two specimens of *C. pacifica* from the Gulf of California examined externally. According to MacFarland & O'Donoghue (1929) and

MacFarland (1966), *C. pacifica* possesses a stalked receptaculum seminis inserting into the vaginal duct. In contrast, *C. lucea* has a serially arranged sperm receptacle which is situated in the proximal portion of the oviduct (Fig. 3). The penis papilla is entirely unarmed in *C. pacifica*, while an apical cuticle is present in *C. lucea*. These external and genital differences clearly indicate that the two species are distinct. No clear differences regarding digestive, central nervous and excretory features can be recognized between *C. lucea* and *C. pacifica*.

Adult *C. evelinae* appear to have fewer gills per row than even juvenile *C. lucea* (7 *vs*. 9-14; Marcus, 1958, 1959; this study). Small "central" gills were described for both species (Marcus, 1958, 1959), but they are absent in smaller specimens of *C. lucea* examined during this study. Gill glands situated at the base of central gills were only known to occur in *C. evelinae* (Marcus, 1958; 1959). However, larger specimens of *C. lucea* examined during this study possess a nearly continuous row of numerous gill glands. Regarding reproductive organ systems, the Brasilian *C. evelinae* comes close to *C. lucea*. Both species have an allosperm receptacle in an unusual proximal position. It is a short stalked sac in *C. evelinae*, while in *C. lucea* it is bulbous and arranged serially. A cuticular armature of the penial papilla shown for *C. lucea* in the present study was mentioned to be absent in a histological study on *C. evelinae* by Marcus (1958). *Corambe evelinae* was said to have a stomachal cuticle and a short folded caecum (Marcus, 1958). Both structures require confirmation and are absent in *C. lucea*. Thus, it seems justified to keep *Corambe lucea* Marcus, 1959 as a separate species.

Comparative anatomy

The Corambidae are enigmatic due to a mosaic of characters either appearing plesiomorphic within the nudibranchs or highly derived (Millen & Nybakken, 1991). Having found new corambid species showing transitional stages (Martynov, 1994a), Martynov (1994b, 1995) regarded the Corambidae as derivatives of onchidorid ancestors within an evolutionary scenario with a high extent of progenesis. Delayed ontogeny might explain some of the most aberrant characters of corambids, i.e. the ventral position of anus and gills, but it is an evolutionary process which *per se* does not allow phylogenetic conclusions. Aberrant corambid organ systems, i.e. digestive system, genitalia, CNS, gills with annexed organs, and circulatory system, require detailed examination and critical homology analysis before being used for phylogenetic purposes. Therefore, in the following, main organ systems of *C. lucea* are discussed comparatively with other known corambid species.

Stomach, caecum and intestine. Corambe pacifica and *C. evelinae* are described as having a "dorsal stomach" clearly separated from the digestive gland and to possess a caecum (MacFarland & O'Donoghue, 1929; Marcus, 1958) which is a transformed remnant of the right digestive gland with opening into the stomach (Schmekel & Portmann, 1982; Schmekel, 1985). In *C. lucea*, however, the stomach is nearly completely fused with a large central cavity of the digestive gland. By histological means, only small remainders of ciliated stomach epithelium have been found. Dorsally rising from the digestive gland cavity, the proximal strongly muscular portion of the intestine is swollen, thus resembling the structures reported from *C. pacifica* and *C. evelinae*. This swollen portion, however, consists entirely of intestinal tissue without any trace of further differentiation into a caecum. This interpretation is supported by ontogenetic studies on *Corambella steinbergae* (as *Doridella*). Bickell *et al*. (1981) showed ciliated vestibule cells to be the only remains of the larval stomach in postlarval individuals. Merging with cells of the left digestive gland they form the digestive gland cavity, "ventral stomach", also found in *C. lucea*. In contrast, the swollen proximal intestine, "dorsal stomach", of *C. steinbergae* derives from cells from the proximal larval intestine, not from the larval stomach (Bickell *et al*., 1981). A right digestive gland is mentioned to be present throughout larval development in *C. steinbergae* (Bickell & Chia, 1979), but no information was given on its presence or development into a caecum within postlarval stages (see Bickell & Chia, 1979; Bickell *et al*., 1981). As mentioned, in adult *C. lucea* no caecum has been found and its presence in adult *C. pacifica* and *C. evelinae* thus may also be doubted. The stomachal ("cardiac") cuticle mentioned for *C. evelinae* by Marcus (1958) is very unusual for nudibranchs and requires histological confirmation.

Digestive gland and dorsoventral muscles. The digestive gland of *C. lucea* is compact, but peripherally separated into five, in some specimens only into three lobes (not considering the more or less superficial division of the posterior lobe by the intestine and kidney). Three or five digestive gland lobes are known for all corambid species for which this aspect has been studied except from *Loy meyeni* and *Proloy millenae*: the latter have holohepatic digestive glands not separated into lobes (Martynov, 1994a) as is observed for Doridoidea and *Bathydoris*.

Redescribing *C. testudinaria*, Garcia *et al*. (1990) first mentioned the presence of a pair of dorsoventral muscular septa between the three digestive gland lobes. In *C. lucea*, three pairs of discrete muscular bundles are present, one pair lateral to the anterior oesophagus, two pairs surrounded by the digestive gland lobes. The pos-

terior pairs seem to coincide with the "coelom partitioning into five parts" mentioned for *C. thompsoni*, *C. pacifica*, *D. obscura* (as *C. baratariae*) and C. *steinbergae* by Millen & Nybakken (1991). In contrast, *Loy* and *Proloy* lack any dorsoventral muscular septa (Martynov, 1994a).

There is evidence that both the co-occurrence of digestive gland lobes and of dorsoventral muscles is not independent: Martynov (1994b, 1995) explained the presence of five digestive gland lobes in corambids by progenesis, reasoning that early stages of the suctorian species *Adalaria proxima* (Alder & Hancock, 1854) have a digestive gland divided into two anterior and two posterior parts which disappear during further development, in contrast to *C. steinbergae* where separation persists in adults. However, his citations of Thompson (1958) and Bickell *et al*. (1981) were inaccurate. Pre- and early postlarval stages of *A. proxima* and *C. steinbergae* have compact, sac-like left digestive glands (Thompson, 1958; Bickell *et al*., 1981) which undergo rapid proliferation forming eventually a five-lobed digestive gland in the latter species (see Bickell *et al*., 1981). The corambid digestive gland thus has holohepatic larval anlagen and in adults always remains compact in the center. Peripherally, corambids possessing dorsoventral muscle-bundles have digestive gland lobes around these muscles, while *Loy* and *Proloy* lack both dorsoventral muscular bundles and digestive gland lobes. Finally, the digestive gland is shown to be easily displaced by the growth of gonads and female gland mass in mature *C. lucea*. The posterior, unpaired lobe is more or less superficially divided into halves by the kidney and intestine. This division seems to be due to simple overgrowing. Therefore, the lobed digestive gland of most corambids is considered to be just a consequence of a normal holohepatic digestive gland growing around the dorsoventral muscles.

Reproductive system. The reproductive system of *C. lucea* generally agrees with the usual triaulic doridoidean type. A bursa copulatrix is located at the distal part of the vaginal duct. However, the proximal allosperm receptacle of *C. lucea* differs in lacking muscular layers and in its aberrant position: it is serially arranged within the proximal oviduct, not connected to the vaginal duct as usual. A receptacle situated at the proximal oviduct, although not serially arranged, was also reported from *C. evelinae, Doridella burchi, Loy meyeni* and *Proloy millenae* by Marcus (1958), Marcus & Marcus (1967) and Martynov (1994a), respectively. Some other corambids, i.e. *C. pacifica* and *C. testudinaria*, were explicitly mentioned to have a receptacle at the vaginal duct. A receptacle at the proximal oviduct seems also present in a few other suctorian species like *Onchidoris neapolitana* (delle Chiaje, 1841) and

Adalaria jannae Millen, 1983 (Schmekel & Portmann, 1982; Millen, 1983); this unique feature thus appears to be distributed through all suctorian families.

CNS. The interpretation, development and homology of ganglia within the Nudibranchia recently has been subject to controversy (i.e. Page, 1992a,b *vs*. Carroll & Kempf, 1994 *vs*. Ruthensteiner, 1999). There is accordance between these and earlier studies (Thompson, 1958; Bickell & Kempf, 1983; Kempf *et al*., 1987) regarding the "cerebropleural" complex of most adult nudibranchs to contain cerebral, pleural and a differing number of visceral loop ganglia. In juvenile and adult *C. lucea*, however, the cerebral, pleural and pedal ganglia are separate from each other. One pair of each cerebropedal, cerebropleural and pleuropedal connectives confirms the identity of these main ganglia (this study). The pleural ganglia may also contain certain ganglia from the visceral loop. The latter is short with a small swelling, probably a visceral ganglion, close to the right pleural ganglion. This situation agrees with that described in great detail for *Corambe pacifica* by MacFarland & O'Donoghue (1929). Separate cerebral and pleural ganglia were also mentioned for adult *Corambe thompsoni*, *Loy meyeni* and *Proloy millenae* (Millen & Nybakken, 1991; Martynov, 1994a). The situation in adult *C. steinbergae* is identical to that of *C. lucea*; cerebro- and pleuropedal connectives confirm the identity of separate cerebral, pleural and pedal ganglia (this study). During larval ontogenesis, Bickell & Chia (1979) described the cerebral and pleural ganglia of *C. steinbergae* (as *Doridella*) as having separate anlagen and not fusing during further development. A separate origin but later concentration was mentioned for *Adalaria proxima* by Thompson (1958). However, both studies only show few discrete stages of larval development. The identity of cerebral and pleural ganglia was not confirmed by detecting both cerebropedal and pleuropedal connectives. Ruthensteiner (1999) showed the development of cerebral and pleural ganglia from a common anlage in ellobiid pulmonates. Critically revising ontogenetic studies on nudibranchs (i.e. Page 1992a,b; Carroll & Kempf, 1994), he concluded that this type of development is found in all Euthyneura. If so, the cerebral and pleural ganglia of *C. steinbergae* also have a common anlage ("cerebral" ganglia of Bickell & Chia (1979)). During later ontogenesis, the pleural ganglia separate from the cerebrals and fuse with ganglia of the visceral loop, the latter being the "pleural" ganglia of Bickell & Chia (1979).

In contrast to other corambids, adult *Corambe testudinaria* have fused cerebropleural ganglia with cerebropedal and pleuropedal connectives clearly illustrated by Fischer (1891: pl. 10, fig. 22). The fused condition in *C. testudinaria* was confirmed by García *et al*. (1990).

Martynov (1994b, 1995) mentioned the cerebral and pleural ganglia of *C. burchi* to be "considerably fused". No information is available on other corambids.

Gills. According to García & García-Gómez (1990), the possible homology of corambid gills with those of Phyllidiidae or "typical" doridoideans was still unresolved. The pectinate shape and structure of the gills of *C. lucea*, although arranged in ventrolateral rows, resemble the mediodorsal gills of the suctorian species *O. bilamellata* described by Potts (1981). Both species possess trabecules within the gills and retractory muscles. Transitional stages found by Martynov (1994a), i.e. *Loy meyeni* with dorsal anus and gills within a pouch and *Proloy millenae* with posteroventral anus and gills within a notal groove, suggest an evolutionary displacement of ancestrally dorsal gills to a ventral position within the corambid clade. This evidence leaves no doubt about the homology of ventral corambid gills and the corresponding dorsal organs in other Doridoidea.

In contrast, the simple, flap-like ventrolateral gills of *Phyllidia flava* Aradas, 1847 (= *P. pulitzeri*) structurally differ from the pectinate and more elaborated doridoidean gills, and therefore were regarded as secondary structures not homologous to the primary gills of Anthobranchia (as Doridacea) by Wägele (1984). Based on these structural differences, the similar lateral position of respiratory organs in phyllidiids and corambids is clearly due to convergence. The gill organization of corambids thus is not an intermediate stage between the typical doridoidean and phyllidiid situation as taken into consideration by García & García-Gómez (1990).

Gill glands. At the bases of the gills of *C. lucea*, ball-like multicellular gill glands open with discrete ducts (Fig. 9). These gill glands closely resemble the gill glands of *Archidoris pseudoargus* (Rapp, 1827) and *Onchidoris bilamellata* (L., 1758) (see Potts, 1981) and other doridoideans (Wägele, 1998) in their position relative to the gills and histological structure. Therefore, they are considered to be homologous organs also supporting the homology of the associated gills.

In phyllidiids, there are no glands comparable to the corambid gill glands at the bases of the lateral gills. Wägele (1984) reported a compact gland within the posterior visceral cavity and connected to the proximal ureter from *Phyllidia flava*. This organ was regarded as a gill gland homologous to that found in *Aegires*, and, due to the similar position, to those of other dorids (Wägele, 1998). The remainder of a gill gland in a postero-dorsal position in *Phyllidia flava* indicates that (dorsal) primary gills were ancestrally present in Phyllidiidae (but lost during evolution), and, since the gland is not related to the lateral respiratory organs, confirms the secondary nature of the phyllidiid gills.

Circulatory system. The corambid circulatory system was described from *Corambe testudinaria* by Fischer (1891). It was similar to that of doridoideans in having a pair of mantle sinuses entering the atrium laterally and a pair of efferent branchial vessels entering the atrium more posteriorly. It was described to differ mainly in the separate openings of the corambid efferent vessels, while "typical" doridoideans have one common terminal opening inserting into the atrium (Wägele, 1984; García & García-Gómez, 1990). The present study, however, shows *C. lucea* to have 1) two pairs of lateral sinuses (pedal and pallial) inserting with separate ducts into the atrium anteriorly, and 2) branchial vessels inserting terminally into the atrium with one common opening. A separate pedal sinus is also present in the cryptobranch dorid *Archidoris pseudoargus* but fuses with the larger pallial sinus some distance before entering the atrium (Potts, 1981). In *Platydoris argo* (L., 1767) the pedal and pallial sinuses are separate until opening into the atrium next to each other (as ventral and auricular veins) as described in great detail by García & García-Gómez (1990). The common insertion of the efferent branchial vessels of *C. lucea* agrees with the situation reported for *Onchidoris bilamellata* and *A. pseudoargus* by Potts (1981), for *Discodoris atromaculata* (Bergh, 1880) by Jonas (1985), and schematically outlined for dorids by Wägele (1984). Therefore, a general homology of the corambid circulatory system with that of doridoideans can be assumed. The phyllidiid circulatory system was regarded to be homologous to the mantle sinuses of the doridoidean bauplan, while the doridoidean branchial system was completely lost (Wägele, 1984).

Conclusions on the systematic position of the Corambidae

Corambe lucea and other corambids are true Nudibranchia. As shown herein they share four of the five autapomorphies of the group resulting from the cladistic analysis by Wägele (1997) and Wägele & Willan (2000): reduction of the shell, visceral ganglion on the right side of visceral loop, pericardial complex orientated in longitudinal direction, and rhinophores with a solid axis. Only special vacuole cells have not been detected so far. *Corambe lucea* shares only one of the three autapomorphies of the Anthobranchia (= Ctenidiacea; see Wägele, 1997; Wägele & Willan, 2000): the notum overgrows the head. A caecum is definitely absent but may have been secondarily lost as in several other anthobranch groups (e.g. Phyllidiidae), and anus and gills are usually not situated mediodorsally but ventrally. However, at least one corambid species, *Loy meyeni*, possesses dorsal anus and gills (Martynov, 1994a), thus an apomorphic ventral shift of these organs within the family is probable. The

oesophagus lacking a cuticle, the triaulic genital system, a blood gland situated near the head region, and the presence of gill glands clearly confirm the corambids as members of the Doridoidea as characterized by Wägele (1997) and Wägele & Willan (2000). Two unique and complex synapomorphies ("presence of a dorsal buccal pump" and the shape of the "large first lateral teeth with rectangular base and long, denticulated hook") unite the doridoidean families Onchidorididae and Goniodorididae with Corambidae to the monophyletic group Suctoria (see Millen & Nybakken, 1991). Two recent cladograms show suctorians as the sister-group of polycerid nudibranchs (Valdés & Gosliner, 2000; Wägele & Willan, 2000), their systematic position within the Doridoidea is, however, still unclear. Whether corambids are a basal offshoot of the Suctoria (Millen & Nybakken, 1991) or progenetic derivatives of certain onchidorid ancestors (Martynov, 1994b), and the question of the possible sister group of Corambidae remains to be analyzed by phylogenetic means.

The external similarity of Corambidae and Phyllidiidae with ventral gills is clearly due to convergence, since the gills and circulatory systems of both groups differ in structure. Since also other organ systems of Corambidae and Phyllidiidae, in particular the suctorian vs. non-suctorian pharyngeal complex, are very distinct (see Martynov, 1994b, 1995), there remains no indication for a sistergroup relationship of these two groups. As shown above for Corambidae, also the Phyllidiidae are true doridoideans having all autapomorphies of the group indicated by Wägele & Willan (2000) (for detailed phyllidiid anatomy see Wägele, 1984, 1985; Fahrner & Schrödl, 2000). Therefore, there is not any reason either for the placement of Corambidae and Phyllidiidae at the base of the Anthobranchia nor for their ranking as orders by Baranetz & Minichev (1994, 1995).

Acknowledgements

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