

CLASSIFICATION OF THE ASCOTHORACIDA (CRUSTACEA)

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Abstract.—The order- and family-level classification of the maxillopodan crustacean superorder Ascothoracida is revised in light of recent advances in taxonomical and morphological knowledge of this group. It is divided into two orders and six families, two of which have two subfamilies. New taxa proposed are the orders Laurida and Dendrogastriida (which supersede the suborders Lauroidida Wagin and Synagogoidida Wagin), the family Ascothoracidae, and the subfamilies Introcorniinae and Ulophysematinae.

The Ascothoracida consist of about 70 described species of parasites of echinoderms and anthozoans. Their taxonomic rank and relationship to other maxillopodan crustaceans, especially to the Cirripectida, have been interpreted differently (e.g. Grygier 1983b, Boxshall 1983, Boxshall and Lincoln 1983). Here they are considered a superorder coordinate with the Cirripectida and the Facetotecta ("Hansen's y-larvae") within the maxillopodan subclass Thecostraca (classification of Grygier 1985a).

Wagin (1976) divided the Ascothoracida, considered by him an order of the Entomostraca, into two suborders: Lauroidida for most of the anthozoan parasites; and Synagogoidida primarily for the echinoderm parasites, but *Synagoga mira* Norman, the type of its genus, infests an antipatharian coral. Wagin's arrangement of Gruvel's (1905) four families and their contained genera follows:

- Lauroidida—Lauridae: *Laura*, *Bacca-laureus*, *Gorgonolaureus*
- Petrarcidae: *Petrarca*
- Synagogoidida—Synagogidae: *Synagoga*, *Ascothorax*, *Parascothorax*
- Dendrogasteridae (sic): *Ulophysema*, *Dendrogaster*

Numerous new species and genera have been described since 1980, mostly by the present author, and the family Ctenosculidae, previously thought to be molluscan, has been transferred to the Ascothoracida (Warén 1981, Grygier 1983d). After the separation of the crinoid-infesting *Waginnella* from *Synagoga* (Grygier 1983a), Wagin's suborders could no longer logically be used if the basic, apparently sound division by host phylum were to be preserved. *Synagoga*, now limited to anthozoan parasites, may reasonably be transferred to the other suborder, but both subordinal names would then come to apply to the old Lauroidida, and the remaining portion of the former Synagogoidida would be left nameless. The recent addition of several genera of gorgonian parasites to the Synagogidae (Grygier 1981, 1984a; Moyse 1983; Lowry 1985) makes the need for an ordinal revision more pressing, and it has also exacerbated the paraphyletic nature of the Synagogidae, which was already evident in Wagin (1976) (defined by possession of a generalized body plan).

The present paper revises the ordinal and familial classification of the Ascothoracida in a manner consistent with current morphological knowledge of the animals (Grygier 1984b) and seeks, as far as possible, to employ monophyletic taxa.

Table 1 is a character state matrix for the genera of Ascothoracida described through early 1986. A very high level of convergence is evident, probably because most of the apomorphic states are easily duplicated reductions associated with parasitism. Therefore, one of the preconditions for a meaningful cladistic treatment, the assumption of relatively rare convergence, is not met. Despite this limitation, several apparently monophyletic taxa have been identified. However, the family Synagogidae, as defined below, and thus also the order Laurida, may still be paraphyletic due to: 1) the near absence of synapomorphies between *Waginella* and other genera, and 2) the possibility that one or more of the advanced synagogid genera, such as *Thalassomembracis*, form the sister group of the Lauridae. Despite these faults, which may eventually be correctable, I believe the following classification of the Ascothoracida to be an improvement over its predecessor, and, aside from possible further subdivision of the Synagogidae, it will serve to place numerous undescribed species and genera now in preparation.

Class Maxillopoda Dahl, 1956
Subclass Thecostraca Gruvel, 1905, sensu
Grygier (1985a)
Superorder Ascothoracida
Lacaze-Duthiers, 1880

Diagnosis. — Bivalved crustaceans (valves often fused in females), diverticula of midgut and gonads in carapace. Primitively with 11 free trunk segments, first 6 with biramous thoracopods, seventh with biramous or uniramous penis in both sexes, last with movable furcal rami. Eyes usually absent. Frontal filaments often present, sometimes combined with uniramous antennae(?) into sensory organs, better developed and plumose in males. Antennules primitively 6-segmented, prehensile, with claw guard and movable claw on sixth segment, setae on fourth, fifth, and sixth. Antennae usually

absent. Labrum conical or pear-shaped, sheathing other mouthparts to form oral cone; maxillae usually with movable subterminal hooks. Female gonopores and often filamentary appendages at base of first legs. Thoracopods primitively paddle-like and setose, usually abutting medially, with 2-segmented exopods, 3-segmented endopods (2-segmented in legs 1 and 6). Seminal receptacles usually in coxae of legs 2–4 or 2–5. Furcal rami blade-like, unsegmented, with various arrangements of terminal and medial setae, primitively a setal fan. Commonly a pair of posteroventral telsonic spines. Apparently gonochorists (Grygier 1987) or (Petrarcidae) simultaneous hermaphrodites. Eggs and larvae usually brooded under carapace; larvae include nauplii and bivalved, “ascothoracid larvae.” Parasites of echinoderms and anthozoans.

Remarks. — Features, especially of the appendages, are modified or reduced in various ways in different ascothoracidans as indicated in the following diagnoses.

Order Laurida, new order

Diagnosis. — Parasites of Anthozoa (except *Waginella*, ectoparasitic on crinoids). Adult morphology highly variable.

Family Synagogidae Gruvel, 1905

Diagnosis. — Parasites of antipatharians, octocorals, and stalked crinoids. Main body and appendages in general plesiomorphic (see above). Carapace bivalved or dorsally fused and expanded into stiff-walled brood chamber (latter correlated with vertical cephalic attachment zone and unpaired dorsal humps or horns on thorax). Fifth antennular segment with several to many setae (but 0–2 in *Thalassomembracis*); sixth with proximal sensory process, usually with aesthetasc and 3 setae (less well developed in *Thalassomembracis* and *Waginella*). Antenna(?)–frontal filament complexes present, best developed in males. Mandibles

Table 1.—Character state matrix for the genera of Ascothoracida (adult females unless otherwise noted). List of symbols: 0, plesiomorphy; 1–3, apomorphies; +, present, –, absent; /, variable within genus; ?, uncertain.

Character states	Genera ¹																U	Bi	D
	W	S	G	Is	Ca	T	L	Ba	Zo	Po	In	Pe	Zi	Pa	A	Ct	E		
Carapace bivalved (0) or univalved with restricted aperture (1)	0	0	1	1	1 ²	1	1	1	1	1	0	0	0	1 ²	1	1	1	1	1
Cephalic attachment zone to carapace dorsal or anterodorsal (0), anterior and vertical (1), or anterior and inverted (2)	0	0	1	1	1	1	2	2	2	2	1	0	0	1	1	2	2	2	0
Antennules 6-segmented (0), 5-segmented (1), 4-segmented (2), or reduced or vestigial (3)	0	0	0	0	0	0	3	3	3	3	1	1	1	1	1	3	3	3♀	2
Plumose appendage (antenna?) associated with frontal filament (♂ and/or ♀)	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
Oral cone "normal" (0), with long languette (+), or with reduced or missing mouthparts (1)	0	+	+	+	+	+	0	1?	0	0	0	1	1	0	0	0	1	1	1
Maxillae bifid (+) or not (–)	–	+	+	?	+ ³	+	+	+	+	+	+ ³	–	–	+	+	+ ³	–	+	+
Thorax "normal" (0), greatly enlarged and/or with processes (1), or with reduced segmentation (2)	0	0	1	1	1	1	1	1	1	1	0	2	2	1	1	1	1	1	2
Filamentary appendages	+ ⁴	–	–	+	+	–	–	+	+	+	–	–	–	+	±	+ ⁴	–	–	–
Thoracopods biramous and paddle-like (0), leaf-like with reduced rami (1), or uniramous (2)	0	0	0	0	0	0	2	2	2	2	2	2	2	1	1	1	1	2	– ⁵
Six pairs of thoracopods (0), some absent (1), or all absent (2)	0	0	0	0	0	0	0	0/1	1	1	1	0/1	1	0	0	0	0	1	2♀ ⁵
Seminal receptacles	+	+	+	+	+	+ ⁶	+	+	+ ⁶	+	+	+ ⁶	+ ⁶	+	+	+	–	–?	1♂
Abdomen 5-segmented (0), clearly 4-segmented (1), or further reduced (2)	0	0	0	0	0	0	1	1	1	1	0	2	2	0	0	1	1	2	2
Penis biramous (0) or uniramous (1) (esp. ♂♂)	0	0	0	1	0	1	1♀	1	1	1♀	0	0	1	1	1	?	1	1	1
Telsonic spines large (0) or minute or absent (1)	0	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Furca forming a tail fan (0), with setose rami but no fan (1), or reduced or absent (2)	0	0	0/1	0	0	1	1	1	1	1	1	2	2	1	1	1	1	2	2
Simultaneous hermaphrodites	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	?	–	–	–
Nauplii with strong endites (0) or not (1)	?	0	1	?	1	1	0	0	0	0	?	0	0	1	1	?	1	1	1
Nauplii with biramous antennae and mandibles (0) or not (1)	?	0	0	?	0	0	0	0	0	0	?	0	0	0	0/1	?	1	0/1	0

¹ Generic abbreviations: W, *Waginella*; S, *Synagoga*; G, *Gorgonolaureus*; Is, *Isidascus*; Ca, *Cardomanica*; T, *Thalassomembracis*; L, *Laura*; Ba, *Baccalaureus*; Zo, *Zoanthoeus*; Po, *Polymarsypus*; In, *Introcornia*; Pe, *Petrarca*; Zi, *Zibrowia*; Pa, *Parascothorax*; A, *Ascothorax*; Ct, *Ctenosculum*; E, *Endaster*; U, *Ulophyesma*; Bi, *Bifurgaster*; D, *Dendrogaster*.
² Large aperture present, but no hinge.
³ Posterior process probably not movable.
⁴ Missed by Grygier (1983a, 1983c).
⁵ While most females of *Dendrogaster* are limbless, a few specimens with uniramous legs have been observed (Grygier, unpubl.).
⁶ Some (Zo) or all (Pe, Zi, 1 species of T) seminal receptacles found in thorax instead of legs.

lanceolate or broad-based but attenuate, with complex but variable medial armament (little armament in *Waginella*). Maxillules blunt with one or more longitudinal comb-rows of setae (styliform and unarmed in *Waginella*). Maxillar tips variable. Hypopharynx produced into long languette (not in *Waginella*). Filamentary appendages present or not. Large epaulets on thoracome 6 (not in *Synagoga*). Details of penis, telsonic spines, and furca variable.

List of genera. — *Synagoga* Norman, 1888; *Waginella* Grygier, 1983a; *Gorgonolaureus* Utinomi, 1962; *Isidascus* Moyse, 1983; *Thalassomembracis* Grygier, 1984a; *Cardomanica* Lowry, 1985.

Remarks. — *Waginella* is included in this family despite its echinoderm hosts (when known) and its somewhat exceptional mouthparts because it and *Synagoga*, the two most generalized ascothoracidan genera, are in most respects extremely similar and until recently were classified in the same genus (Grygier 1983a).

Family Lauridae Gruvel, 1905

Diagnosis. — Endoparasites or mesoparasites of zoanthids. Female carapace univalved, greatly enlarged relative to body, often with lateral pouches or coils, cephalic attachment zone inverted; males bivalved, much smaller than females. Antennules reduced in females, claw vestigial or absent; male antennules generalized. Oral cone normal. Mandibles usually with medial hairs, maxillules blunt, unarmed, maxillae generalized. Four to 6 pairs of uniramous, segmented legs with short, spine-like setae in females; 6 pairs in males, some biramous. Female filamentary appendages oval, plate-like (absent in *Laura*). Abdomen 4-segmented, last segment sometimes showing partial division. Penis uniramous (often very long in males). Telsonic spines small or absent. Furcal rami with up to 4 terminal setae, usually no medial setae.

List of genera. — *Laura* Lacaze-Duthiers, 1865; *Baccalaureus* Broch, 1929; *Zoan-*

thoecus Grygier, 1985b; *Polymarsypus* Grygier, 1985b.

Family Petrarcidae Gruvel, 1905

Diagnosis. — Endoparasites of scleractinian corals. Carapace of two thick valves armed with spines and/or papillae, lacking brood chamber. Antennules 5-segmented, not subchelate, only distal segment well armed. Antennae absent. Oral cone variable; mandibles and maxillules with short, medial cutting edge, rarely unarmed; distal parts of maxillae reduced. Thoracopods uniramous, with few or no setae, first pair reduced or absent, no filamentary appendages. First abdominal segment much larger than others. Penis and terminal abdominal segment variable. Simultaneous hermaphrodites.

List of subfamilies. — Introcorniinae, new subfamily; Petrarcinae Gruvel, 1905.

Subfamily Introcorniinae, new subfamily

Diagnosis. — Carapace spherical with papillae; cephalic attachment zone vertical. Antennular cuticle of even thickness, distal segment generalized. Labrum normal; maxillae with hairy, vestigially bifid tips. Thorax clearly segmented. Thoracopod 1 absent; other 5 pairs segmented, weakly setose, some with seminal receptacles. Abdomen 5-segmented, penis in form of 2 blunt lobes. Furcal rami well developed.

List of genera. — *Introcornia* Grygier, 1983d (type genus).

Subfamily Petrarcinae Gruvel, 1905

Diagnosis. — Carapace ovoid or dome-shaped, with spines and/or papillae; cephalic attachment zone dorsal, horizontal. Basal antennular segments with distinct sclerites; conspicuous armament of fifth segment reduced to claw and claw guard bearing a large seta. Labrum blunt, rear edges widely separated; maxillae forming a short, massive labium. Thoracic segmentation obscure. Five or 6 pairs of unsegmented, un-

armed, usually lobular thoracopods, first pair narrow or setiform when present. Seminal receptacles in thorax. Extremely long and robust penis with short rami or none. No more than 4 abdominal segments, all but first very reduced. Furcal rami vestigial or absent.

List of genera.—*Petrarca* Fowler, 1889; *Zibrowia* Grygier, 1985c.

Order Dendrogastrida, new order

Diagnosis.—Parasites of echinoderms. Carapace valves in females at least partly fused, soft-walled with delicate cuticle, often greatly enlarged. Trunk variable, generalized to extremely reduced. Antennules 4- or 5-segmented and subchelate at some stage of development, or vestigial; proximal sensory process of terminal segment reduced to isolated aesthetasc and seta, aesthetasc ribbon-like in larvae (antennular details to be confirmed in larval Ctenosculidae). Antennae absent. Mandibles and maxillules unarmed, at least medially, when present. Thoracopods leaf-like, uniramous, or absent.

Family Ascothoracidae, new family

Diagnosis.—Bursal parasites of ophiuroids. Carapace in females roughly spherical or ovoid, valves partly fused with pair of thin-walled, dorsal brood chambers; cephalic attachment zone vertical; males bivalved, much smaller than females. Antennules 5-segmented, subchelate, fourth segment usually with toothed process. Labrum normal. Mandibles setiform with distal hairs. Anterior thoracomeres usually greatly swollen with bilateral protrusions. First thoracopods short, uniramous; filamentary appendages often present. Next 4 pairs of legs leaf-like, with short, rounded rami (legs narrow in males, endopod reduced or absent); sixth legs short. Seminal receptacles small, tubular, often only in legs 2–4. Abdomen 5-segmented, sharply bent at segment 4; penis a short lobe, even in

males. Furcal rami elongate, usually with short ventral setae in females, a few distal setae in males.

List of genera.—*Ascothorax* Djakonov, 1914 (type genus); *Parascothorax* Wagin, 1964.

Family Ctenosculidae Thiele, 1925

Diagnosis.—Mesoparasites of starfish. Ovoid carapace with short, posteroventral or ventral aperture. Cephalic attachment zone inverted. Antennules minute or absent. Front side of labrum short. Mandibles apparently absent; maxillae bifid, but not hooked. Thorax enlarged, with humps or long dorsal horns. Thoracopods typically leaf-like, sometimes uniramous; filamentary appendages sometimes present. Abdomen 4-segmented, penis vestigial or absent. Furcal rami large, variable. Adult males unknown.

List of genera.—*Ctenosculum* Heath, 1910; *Endaster* Grygier, 1985d.

Family Dendrogastridae Gruvel, 1905 (name corrected)

Diagnosis.—Female carapace (mantle) produced into large, soft-walled lobes or branches. Antennules 4-segmented, subchelate at some stage of development. Mandibles and maxillules vestigial or absent. Thoracopods short and uniramous, or absent; first pair always absent. No filamentary appendages or seminal receptacles. Abdomen at most 3-segmented, often absent, furcal rami present as unarmed lobes or absent.

List of subfamilies.—Ulophysematinae, new subfamily; Dendrogastrinae Gruvel, 1905.

Subfamily Ulophysematinae, new subfamily

Diagnosis.—Endoparasites of irregular echinoids. Mantle with anterior and posterior lobe and ventral aperture, cephalic

attachment zone inverted. Antennules in adult poorly segmented, with small distal segment and claw. Mouthparts absent except for small labrum. Dorsal horns on first 4 thoracomeres. Four or 5 pairs of short, uniramous limbs with short setae. Abdomen 2- to 3-segmented, with or without fixed furcal lobes. Adult males unknown.

List of genera. — *Ulophysema* Brattström, 1936 (type genus).

Subfamily Dendrogastrinae Gruvel, 1905

Diagnosis. — Endoparasites of starfish. Female mantle developed into pair of posterior lobes or bilateral system of branches with very small aperture. Cephalic attachment zone anterodorsal. Males bivalved, each valve with posterior protrusion; living in female brood chamber. Antennules and maxillae well developed in adults; third antennular segment lacking process, but usually with 1 or 2 spine-like setae opposing claw. Thorax and abdomen obsolete, sac-like, limbs generally absent, no furca.

List of genera. — *Dendrogaster* Knipovich, 1890 (subjective synonyms: *Myriocladus* Okada, 1925 and probably *Laocoon* Nierstrasz and Entz, 1922); *Bifurgaster* Stone and Moyse, 1985.

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Note added in proof

The new genus *Paremedius* Stone, 1987 (*Journal of Natural History* 21:219–224) belongs to the Dendrogastrinae. I regard it as a synonym of *Bifurgaster*, and in all described features it agrees with that genus in Table 1.



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