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Branchiura (Crustacea) – Survey of Historical Literature and Taxonomy

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> Abstract

The Branchiura (carp lice) is a small group of parasitic Crustacea found mainly on freshwater fish comprising the four genera *Argulus*, *Dolops*, *Chonopeltis* and *Dipteropeltis*. The earliest descriptions of "carp lice" dates back to 10th century China, and several descriptions were made in the beginning of the "modern age" of Zoology beginning in the 18th century. However, the last genus to be described was *Dipteropeltis* as late as in 1912. While a few species like *Argulus foliaceus*, *A. japonicus* and *Dolops ranarum* are fairly well-known, most Branchiura species remain more or less uninvestigated. As the literature is far spread and often hard to access, this survey aims to give an overview of the most important available historical literature on morphology, and systematics / nomenclature in a chronological order for each of the four genera, to the hopeful benefit of Branchiura researchers.

> Key words

Crustacea, Branchiura, *Argulus*, *Dolops*, *Chonopeltis*, *Dipteropeltis*, review.

1. Introduction

The Branchiura are fascinating Crustacea not only able to attach to the slippery sides of freshwater fish, but also able to swim freely to find another host, should the situation call for it. Comprising around 210 species in four genera (*Argulus*, *Dolops*, *Chonopeltis*, and *Dipteropeltis*), it belongs to the smaller crustacean taxa (Martin & Davis 2001). The Branchiura are ectoparasitic on primarily freshwater fish, although a few species of *Argulus* have been described from marine fish and scattered reports of Branchiura on tadpoles, salamanders and even alligators can be found (Ringuelet 1943; Piasecki & Avenant-Oldewage 2008).

Branchiura is not in the main stream of research on crustacean systematics and phylogeny. Nevertheless there is much scattered information available in the literature but it mostly consists of single species descriptions. In order to facilitate further research on the systematics of Branchiura, I here present aspects of the historical background and literature on the group, firstly focusing on the Branchiura as a group, the name's history and origin and the suggested systematic affinities. Secondly, I will give a short historical introduction to the nomenclature of each of the genera and give a chronological overview of the most important literature on them, concentrating on contributions to the knowledge of morphology, ontogeny and phylogenetic systematics. All relevant literature of the purely parasitological and pathogenic aspects of the Branchiura was recently reviewed by Piasecki & Avenant-Oldewage (2008).

2. Material and methods

Adult *Argulus foliaceus* material was collected in Utterslev Mose (N. part of Copenhagen, DK) mainly from host specimens of roach (*Rutilus rutilus* (L.)), carp bream (*Abramis brama* (L.)), and rudd (*Scardinius erythropthalmus* (L.)) caught in gill-nets in 2005–06. Larvae were collected from an exhibition tank at

the Danish National Aquarium, Charlottenlund DK, with a plankton net (mesh size 63 μm). Specimens of *Dolops ranarum* and *Chonopeltis australis* were collected in South Africa and all specimens for SEM were fixed using standard methods (see Møller et al. 2007, 2008 for details & locations). For comparison, additional specimens of *C. australis* (col. no: 1975-1092) as well as specimens of *Dolops geayi* (col. no. 1930-8-27) and *Dipteropeltis hirundo* (col. no. 1974-839) from the Natural History Museum, London, were depicted. The photo of *D. carvalhoi* in Fig. 1B was provided by Mr. Tomonari Kaji, Shizuoka University, Japan.

3. Brief account of morphology

As many other ectoparasitic Crustacea, the Branchiura have dorso-ventrally flattened bodies and normally they range between 4 and 15 mm in size (*Dipteropeltis hirundo* and *Dolops longicauda* up to 30 mm) (Fig. 1). The carapace shape is variable (a dorsal cephalic shield is always present), ranging from almost circular (in *Dolops discoidalis*), over clover-leaf shaped in *Chonopeltis* (Fig. 1C), to drawn out into two long lobes in *Dipteropeltis* (Fig. 1E–F). Four pairs of thoracopods for off-host swimming and an unsegmented abdomen with a pair of (in adults) minute furcal rami are always present (Fig. 2A,D,H) (Wilson 1902; Calman 1912; Avenant-Oldewage & Knight 1994; Piasecki & Avenant-Oldewage 2008).

The Branchiura cephalic appendages are highly modified for the parasitic lifestyle. The mouth opening and mandibular gnathal processes are situated at the tip of the so-called mouth cone or proboscis (Fig. 2A) – at least in *Argulus* considered a fusion product of a sternal outgrowth and the labrum (Martin 1932; Gresty et al. 1993). The length of the cone varies between the different genera, being short in *Dolops* and *Chonopeltis*, and longer in *Argulus* and *Dipteropeltis* (Martin 1932; Gresty et al. 1993; Avenant-Oldewage & Knight 1994; Rushton-Mellor 1994c). In front of the mouth cone, a so-called preoral spine can be found in *Argulus* (Fig. 2C) and also in *Dipteropeltis hirundo* (pers. obs. and see Ringuelet 1943). This structure is probably used to penetrate the host's integument and promote haemorrhaging (only documented for a few species of *Argulus*), which the Branchiura subsequently feed on (Swanepoel & Avenant-Oldewage 1992; Gresty et al. 1993).

The Branchiura primarily use the modified first maxillae as a means of attaching to the fish: distal suction-disc-like structures in adults of *Argulus*, *Chonopeltis* and *Dipteropeltis* and stout distal hooks in *Dolops* species (Figs. 1A,C, 2B,G,I). Apart from this, the distal tips of the second maxillae of all Branchiura are equipped with hooks for additional anchoring capability. Several detailed accounts of the precise morphology of the cephalic appendages are available (see, e.g., Gresty et al. 1993; Swanepoel & Avenant-Oldewage 1993; Avenant-Oldewage et al. 1994; Møller et al. 2008; and references below).

4. Literature and historical systematics

The literature on Branchiura stretches back to the earliest descriptions of animals in a "modern" fashion and has been known from literature as early as 1666 (Wilson 1902). It was well-known also to Linné in his Systema Naturae where the later *A. foliaceus* was described as *Monoculus foliaceus* (Linné 1758). According to Piasecki & Avenant-Oldewage (2008) the oldest mention ever of Branchiura dates back to 10th century China, where a monk specifically mentioned the most efficient way of dealing with the "lice" of carps. With all certainty, these "lice" were an *Argulus* species.

4.1. Branchiura as a separate taxon

The name "Branchiura" was coined by Thorell in 1864, but argulids had been known for almost 200 years before this (Thorell 1864). Thorell entered into a debate on the position of the genera *Argulus* and *Gyropeltis* (junior synonym for *Dolops*) within the system of Crustacea, as a reaction to papers by, e.g., Krøyer (1863) and Heller (1857), who had placed the two genera in the siphonostome Copepoda. Thorell did not agree on this and argued for placing the two groups in the Branchiopoda close to the Cladocera; a view also presented by Zenker (1854) (Wilson 1902). Thorell (1864) termed the group Branchiura or gill-tails ("… hemtad från stjertens för dessa djur så karakteristiska betydelse". Author's own translation: "…taken from the characteristic importance of the tail of these animals"; Thorell 1864: 55). Some of Thorell's arguments for not placing the Branchiura in the Copepoda are valid but they were based on a misunderstanding of the morphology of the Branchiura cephalic appendages, mistaking the second maxilla for a maxilliped. Thorell emphasized the presumed respiratory function of the abdomen ("tail"), the non-fused compound eyes, and what he called "the tendency to form a carapace" as justification for grouping the Branchiura and

the Branchiopoda (Phyllopoda in his terminology) (Thorell 1864). His arguments are solely based on what probably are symplesiomorphies and definitions based on "lack of …" statements. The fact that branchiopods do not have thoracopods specialized as maxillipedes is ignored, and the word "maxilliped" is included in the diagnosis of the Branchiura (Thorell 1864). This simple fact would influence the systematic position of the group for almost 70 years.

Claus was an ardent opponent of the Branchiura-Branchiopoda connection, and in his detailed work from 1875, he restated the hypothesis proposed earlier of an affiliation of the Branchiura to the copepods (Claus 1875). He suggested placing the Branchiura in a separate suborder of the Copepoda, with the parasitic and free-living groups as the other suborders; a view supported by Leydig (1889). In 1902 Wilson presented an exhaustive work on all (at the time) 29 known species of *Argulus*, nine species of *Dolops* and the single known species of *Chonopeltis* (Wilson 1902), providing new observations on especially *Argulus*. The work can be considered a milestone in branchiuran literature, although Wilson still regarded the Branchiura as a part of the Copepoda. He also based this on the (erroneous) identification of the first maxilla as being included within the mouth cone, thus making the true first maxilla a second maxilla, and the true second maxilla a maxilliped (Wilson 1902) – a morphology that, if true, would be similar to siphonostome copepods.

Thiele was the first to introduce the interpretation of the cephalic appendages in the group which is now considered as correct (Thiele 1904). He reinvestigated 19 species of *Argulus* (10), *Chonopeltis* (1) and *Dolops* (8) available to him and considered all of the arguments presented for the specific homologization of the cephalic appendages. Thiele was unable to find any evidence for the first maxillae to be included in the mouth cone / proboscis and he also identified the location of the maxillary gland ("Schalendrüse") on the posteriormost of the two appendages between the mandible and the first swimming leg which is thereby suggested to be a second maxilla. Based on these facts, he concluded that branchiurans had no connection with Copepoda (or phyllopod branchiopods) and that "...bleibt nur übrig, sie als besondere, den Copepoden und Phyllopoden gleichwertige Gruppe von Crustaceen aufzufassen…" (Thiele 1904: 48) (author's own translation: "… we are left with no other possibility than to consider it [i.e. Branchiura] as a particular group of crustaceans, equal to the phyllopods and copepods…").

Thiele's (1904) conclusions notwithstanding, the Krøyer/Leydig/Wilson theory of the phylogenetic position of the Branchiura was the one adopted by Calman (1909) in the Crustacea section of Lankester's "A Treatise on Zoology". The formal placement of the Branchiura within the Copepoda was thus maintained until the early thirties (see, e.g., Cunnington 1913; Wilson 1916, 1920a, 1921, 1923, 1924; Brian 1924). Martin (1932) was probably inspired by Thiele's (1904) work to investigate the mouth cone in *A. viridis* and she critically evaluated the arguments for Branchiura-Copepoda relationship and concluded as Thiele: No evidence from ontogeny or morphology pointed to the first maxilla being situated within the mouth cone. It was clearly shown that the first maxillae are free and movable in the first larval stages and during ontogeny, the proximal part develops into the suction discs of the adult (Fig. 3C) (Martin 1932). The notion of a fusion between the first thoracic segment and the cephalon was then also necessarily invalidated. Martin (1932) suggested raising the Branchiura to subclass level, equal to the Copepoda, following Thiele's conclusion (Martin 1932).

The formal removal of the Branchiura from the Copepoda was not adopted for more than 10 years (e.g., in the papers by Stekhoven 1937 and Brian 1940). Meehan (1940) referred to Argulidae as a family of Copepoda, but recognized the presence of two pairs of maxillae, whereas Ringuelet (1943) completely separated Copepoda and Branchiura, specifically mentioning Martin (1932) as reference. Brian (1947) listed Copepoda and Branchiura at the same systematic level in his review of the Branchiura collection in the National Natural History Museum of Argentina, thus acknowledging the formal separation.

Since then, with very few exceptions (e.g., Martinez 1952; Ramakrishna 1952; Barnard 1955) all major works on Branchiura have accepted Branchiura as separate from Copepoda. Importantly, the subclass Branchiura was adopted by Fryer in his papers on African Branchiura (Fryer 1956). The review by Yamaguti (1963) contained a very extensive literature list of Branchiura and parasitic Copepoda, but unfortunately the taxonomy contained in it is flawed and contains severe misunderstandings, e.g., using the two non-valid genera *Talaus* Morereia, 1913 and *Huargulus* Yü, 1939. Monod (1928) had already shown that *Talaus* was a synonym for *Dipteropeltis* and *Huargulus* was shown to be a juvenile *A. japonicus* by Tokioka (1940) (see Fryer 1969 for further clarifications).

4.2. Phylogeny within Branchiura

The internal relationships of the Branchiura have only received fleeting attention, but they were discussed briefly by Fryer (1956). He inferred that *Chonopeltis* and *Dipteropeltis* were "degenerated from an *Argulus*-like ancestor", based on what he considered to be a series of shared so-called reductions in morphology,

e.g., reductions in the setation of the thoracopods, and a reduction of the first antennae in *Chonopeltis* (FRYER 1956, 1969). Unfortunately, the position of *Dolops* was not considered. These inferences are not fully compatible with modern cladistic analyses, and thus not easily applicable to the findings by MØLLER et al. (2008), who presented a phylogenetic reconstruction of the Branchiura based on molecular data. However, the affinity of *Chonopeltis* to *Argulus* was confirmed, as at least one *Chonopeltis* species consistently nested within an *Argulus*-clade, necessarily then questioning the monophyly of the latter. *Dolops* was found to be the sister group to the remaining Branchiura, and while the precise position of *Dipteropeltis* could not be stated (due to lack of material for DNA-analysis), it was tentatively suggested to have an affinity to the *Argulus* + *Chonopeltis* clade (MØLLER et al. 2008).

4.3. What is the closest relative to Branchiura?

The question of the closest relative of the Branchiura was reanimated in 1972 by Wingstrand's hypothesis of a Branchiura + Pentastomida relationship based on very detailed sperm-ultrastructural similarities; e.g., both groups possess a bilateral spermatozoon with a completely reduced free flagellum (see WINGSTRAND 1972 for details). The Pentastomida are parasites in the respiratory tracts of vertebrates and their phylogenetic position has been discussed for many years (see, e.g., OSCHE 1963; SELF 1969; DE OLIVEIRA ALMEIDA & CHRISTOFFERSEN 1999; WALOSZEK et al. 2006). Wingstrand's suggestion of a Branchiura + Pentastomida relationship has found strong support from molecular data by several researchers (such as ABELE et al. 1989; PETERSON & EERNISSE 2001; ZRZAVÝ 2001; LAVROV et al. 2004; LIM & HWANG 2006) and for the first time also the relationship was supported with in-group sampling of both taxa, suggesting that Pentastomida probably is not an ingroup branchiuran (MØLLER et al. 2008). The name Ichthyostraca was suggested for this clade by ZRZAVÝ (2001). Spermatological data is seemingly the only morphological data able to support the Ichthyostraca (RILEY et al. 1978; STORCH & JAMIESON 1992). On the other hand, several authors have argued strongly for placing the Pentastomida far away from the Crustacea as the sister-group to the Euarthropoda, e.g., MAAS & WALOSZEK (2001) and WALOSZEK et al. (2006), leaving the Branchiura + Pentastomida open for discussion.

4.4. *Argulus*

Figs. 1A, 2A–C, 3A–C

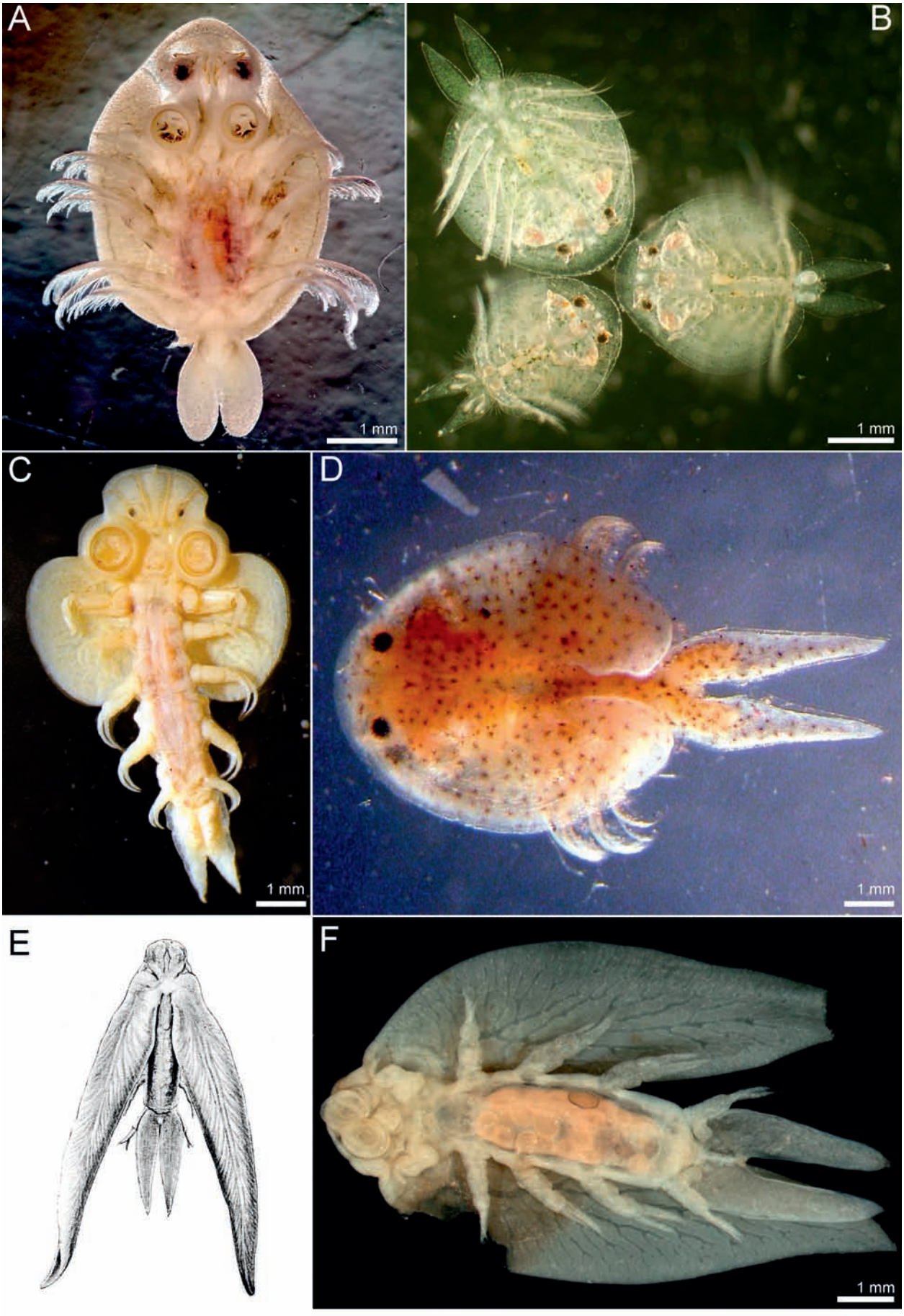
The largest and most diverse genus is *Argulus*. The genus name is attributed to the Danish naturalist Otto Frederik Müller in a work from 1785 (MÜLLER 1785; WILSON 1902). The name is supposedly a diminutive of Argus, a mythical beast from Greek mythology with a hundred eyes, in reference to many omatidia in the *Argulus* compound eyes (WILSON 1902). JURINE (1806) was probably the first to use the name combination *A. foliaceus* in a work presenting data on both morphology and ontogeny.

Several other names for the genus persisted in the literature at that time, e.g., *Monoculus*, *Binoculus*, *Ozolus* and *Agenor*, but Latreille used Müller's name *Argulus* in his chapters for Cuvier's "Règne Animal", specifically mentioning Jurine's work on *Argulus* (CUVIER & LATREILLE 1834) (information partly from WILSON 1902).

LEYDIG (1850) contributed a detailed description of the highly compact nervous system as well as a first description of the genital system in *A. foliaceus*. THORELL (1864) provided one of the first attempts of a systematic definition of the subdivisions in the Branchiura, including a definition of the genus *Argulus*. The larval development of *A. foliaceus*, details of the late embryo as well as the early larvae were given by CLAUS (1875), while LEYDIG (1889) substantially contributed to the knowledge of the microscopic anatomy of *A. foliaceus*, e.g., with new details of the second maxillae suction disc structure, and improved data on the central nervous system.

The works by WILSON (1902, 1904a,b) provided much new data on *Argulus*, e.g., on the differences in the developmental stage at hatching in *Argulus*. The metanauplius larvae of *A. foliaceus* and *A. catostomi* were already known, but the juvenile-like hatching stage in *A. megalops* and *A. stizostethii* were unknown (Fig. 3A,B). Wilson also experimented with the osmoregulatory capacities of *Argulus* by transferring animals directly from fresh to salt water, seemingly not affecting the parasites negatively. However, these experiments were only mentioned in passing and have gone unnoticed since. Furthermore, he also pro-

Fig. 1. A: *Argulus foliaceus*: Ventral view of adult female. **B**: *Dolops carvalhoi*: Ventral view of two females and one male (photo courtesy of Tomonari Kaji, Shizuoka University, Japan). **C**: *Chonopeltis australis*: Ventral view of female (NHM-material spec. no. 1975-1092). **D**: *Dolops geayi*: Dorsal view of female (NHM-material spec. no. 1930-8-27). **E–F**: *Dipteropeltis hirundo*. **E**: Reproduced from CALMAN (1912) showing the dorsal view of the holotype. **F**: Ventral view of paratype specimen (NHM-material spec. no. 1974-839).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vided a rough sketch of the circulatory system as well as an overview of the genital system (Wilson 1902, 1904a,b, 1907).

Thiele (1904) provided important new data in the discussion of the branchiuran systematic affinities with excellent drawings of especially the cephalic appendages, while Grobben (1908) provided a histological account of *A. foliaceus* with special emphasis on the genital system, with remarkably precise drawings. In the field of taxonomy Cunnington (1913) and Monod (1928) described numerous new species of *Argulus* from Africa and provided identification keys. The taxonomy of the American *Argulus* species was covered in a series of papers by Wilson (Wilson 1916, 1920a,b, 1921, 1923, 1924).

The paper by Martin (1932) proved central in presenting some of the only drawings ever published on late embryos of any *Argulus*-species, as well as a precise description of the mouth cone and its ontogeny. With this paper, the discussion of a position of the Branchiura within the Copepoda was finally put to rest (see above).

Stekhoven (1937) provided one of the first "character based" comparisons of African and South American species of *Argulus*, and compared characters of the carapace, maxillae, thoracopods, and the abdomen. Unfortunately, no real conclusions were drawn from the results. The nervous system of *A. foliaceus* was investigated by Zacwilichowska (1948), complementing the works by Leydig (1889) and Martin (1932).

Meehan (1940) reviewed all the specimens in the collection of the United States National Museum and suggested several taxonomic revisions of species described earlier by Wilson. This prompted a rebuke by Wilson who called Meehan's work a "serious encroachment upon the genus" and refuted most of the revisions (Wilson 1944).

The papers by Brian (1947) and Ringuelet (1943; 1948) provided an excellent and rare coverage of the South American species of *Argulus*, and they are of high taxonomical value, with descriptions of, e.g., the almost *Dipteropeltis*-like *A. paranensis*.

In a series of papers from 1956 onward, Fryer contributed with a large amount of so called "biological notes" on distribution and collections, observations on morphology, reproduction, ontogeny and many other aspects of African Branchiura. Fryer (1956) and Fryer (1959) presented data on *Argulus* from Lake Malawi (formerly Lake Nyasa) and Lake Bangweulu, respectively, with descriptions of several new species and detailed notes on ecology and biology. In Fryer (1961b) data on *Argulus* from Lake Victoria was presented along with a comparison of the ecology of *Dolops* and *Argulus*. Collecting data on six species of *Argulus* from the Great Lakes (Kivu, Edward, Albert and Tanganyika) was presented in Fryer (1965a), and a taxonomic revision of the African *Argulus* species along with descriptions of new species from the Nile and Niger River systems was given in Fryer (1965b). In Fryer (1968) most of the knowledge of the African *Argulus* is summarized, and distribution maps, notes on biology and evolutionary considerations are presented.

Histological investigations of the integument and nervous system of *A. foliaceus* were given by Madsen (1964), and Haase (1975a,b) showed that the so-called respiratory areas of the carapace probably do not primarily serve the respiration; rather an osmoregulatory effect / function was suggested.

Shimura (1981) described the larval development of *A. coregoni* and two years later he described its mouth cone morphology (Shimura 1983) as well as the glands associated with the pre-oral spine (Shimura & Inoue 1984).

Shafir & van As (1986) presented key data on the egg laying and development of *A. japonicus* in South Africa, followed by investigations of ecology and life history traits such as fecundity, size distributions and infestation rates of this species by Shafir & Oldewage (1992). Further ontogenetic data was presented by Rushton-Mellor & Boxshall (1994) and Lutsch & Avenant-Oldewage (1995) in descriptions of the larval development of *A. foliaceus* and *A. japonicus*, respectively. A description of the fine structure of the mouth cone, pre-oral spine, and more importantly the development of these structures in *A. japonicus* was given by Gresty et al. (1993).

A complete account of the histology and structure of the male genital system and method of sperm transfer in *A. japonicus* was given by Avenant-Oldewage & Swanepoel (1993), and in a series of papers by Ikuta, the female genital system was described in detail including data on oogenesis and ovary structure (Ikuta & Makioka 1997) and eggshell ultrastructure (Ikuta et al. 1997 and references therein).

Some taxonomic issues of African members of *Argulus* were covered in three papers by Rushton-Mellor, including the description of two new species and an unknown male in Rushton-Mellor (1994a), the redescription of type material and taxonomic revisions in Rushton-Mellor (1994b) and finally an identification key of the African *Argulus* species (Rushton-Mellor 1994c). The lack of an updated taxonomy and general knowledge of the American *Argulus* species was pointed out by Poly (2008), albeit he himself had contributed with new species descriptions, e.g., Poly (2005).

Recently, the gut ultrastructure of larval *A. japonicus* was reconstructed based on sections by Tam & Avenant-Oldewage (2006), who concluded that the first larval stage primarily sustains itself on yolk (no

blood was found in the gut). Møller et al. (2007) discussed aspects of the first larval stage swimming and cleaning behaviour in *A. foliaceus* and reviewed the morphological background and prerequisites for parasitism in stage 1 larvae. The study by Tam & Avenant-Oldewage (2006) was followed by an ultrastructural description of the digestive cells in adult *A. japonicus*, which concluded that the elaborate enteral diverticula are only simple elaborations of the anterior midgut, and not comparable with the midgut glands or hepatopancreas of other Crustacea (Tam & Avenant-Oldewage 2009).

4.5. *Chonopeltis*

Figs. 1C, 2D–G, 3D,F

The exclusively sub-Saharan genus *Chonopeltis* was originally described in Thiele (1900) based on material from Lake Rukwa (on the Tanzania / Zambia border, then a part of German East Africa), with *Chonopeltis inermis* as the type species. Thiele did not give an etymological background, but the name is derived from "Chonos" (funnel / cone) and "Pelta / Pelte" (Greek: small shield), thus meaning cone- or funnel-shaped shield.

Wilson (1902) cited the new genus, but apart from a notice in Thiele (1904) and a single mention of a collection of *C. inermis* specimens by Monod (1928), no new data was published on *Chonopeltis* for almost 40 years (Thiele 1904; Avenant-Oldewage & Knight 1994). Brian (1940) described a single species variant *C. inermis* var. *schoutedeni*, but the material was reinvestigated by Fryer, and published as three separate species, C. *schoutedeni*, *C. congicus* (Fryer 1959) and *C. flaccifrons*, making him the author of more than half of all known species of *Chonopeltis* (Fryer 1960a). The first account of the apparent lacking swimming ability and general inactivity of adults in the genus was given by Fryer (1956), reporting this and many other significant observations on the ecology of *C. inermis*. The species *C. flaccifrons* Fryer 1960a, is interesting as it lacks the, for the genus, characteristic cephalic lobe support rods, suggesting a possible neotenous character state. Four new species were described in Fryer (1964, 1974, 1977) and Boxshall (1976): *C. meridionalis*, *C. elongatus*, *C. minutus* and *C. australis*, respectively, and in Fryer (1977) a key to the species was also given. More species and distribution data were given by, e.g., van As (1986) (*C. fryeri*), van As (1992) (*C. koki*), van As & van As (1993) (*C. inermis*), Avenant-Oldewage (1991) (*C. victory*), van As & van As (1996) (*C. lisikili*), and van As & van As (1999a) (*C. liversedgei*). Based on these papers and the species compendium given in Avenant-Oldewage & Knight (1994) the genus currently counts 15 species (14 according to van As & van As 1999b).

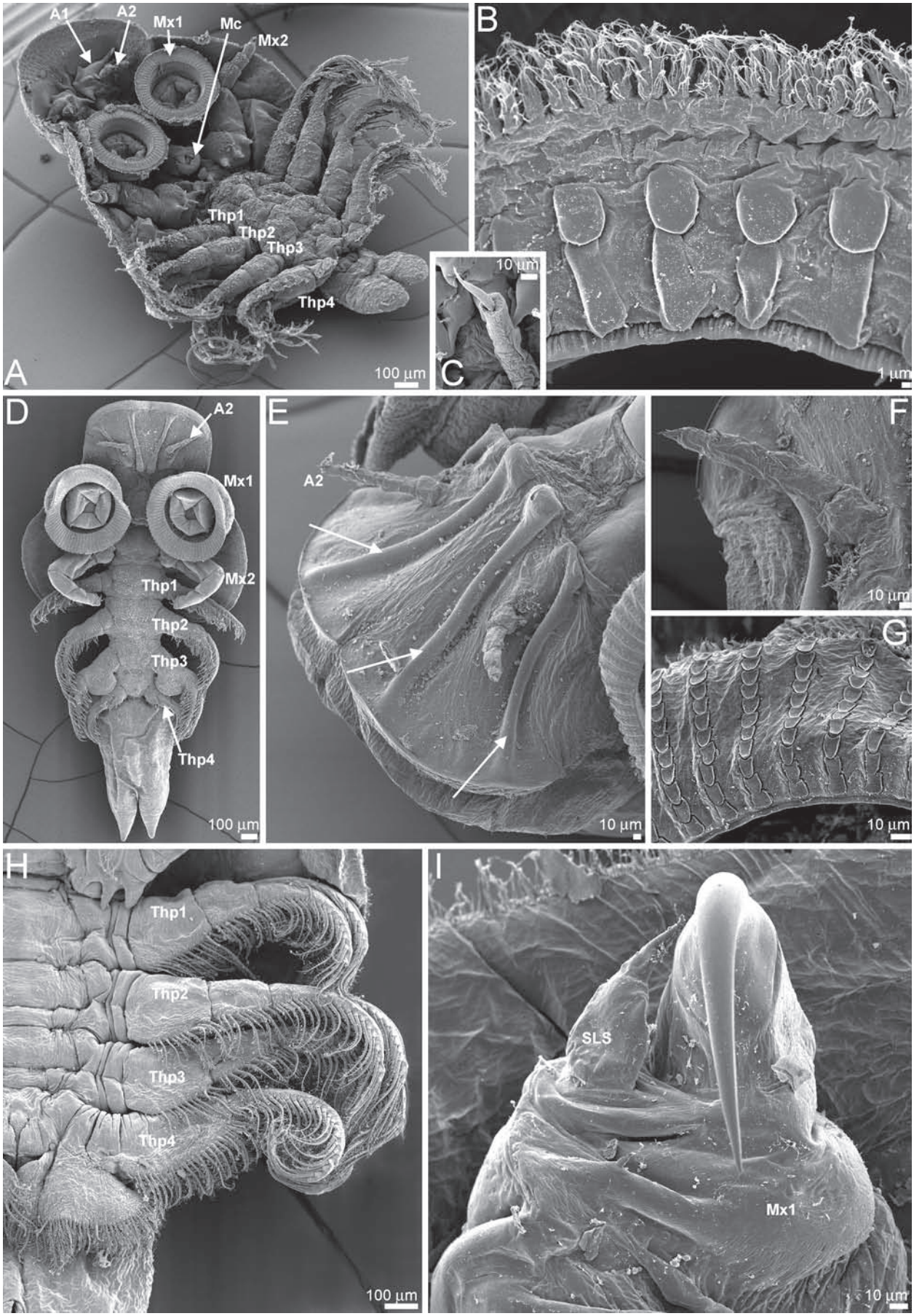
The first descriptions of the larval stages of *C. inermis* (Fryer 1956), *C. brevis* (Fryer 1961a) and *C. minutus* (Fryer 1977) are particularly interesting, as they showed that *Chonopeltis* larvae look significantly different from the already known larvae of *Argulus* and *Dolops*, in not showing metanauplius or juvenile-like morphology (Fig. 3D,F) (see also Avenant et al. 1989b; Møller et al. 2007, 2008).

Details of the cephalic appendages of *C. australis* were given in van Niekerk & Kok (1989), while the functional morphology of the foregut and digestive tract of this species were described using histological methods by Avenant-Oldewage et al. (1994) and Swanepoel & Avenant-Oldewage (1993). A general investigation of the external morphology of *C. victory* was done by Luus-Powell & Avenant-Oldewage (1996), while new ontogenetic data on the atypical *Chonopeltis* larvae were presented by van As & van As (1996) including also the hitherto only published SEM micrograph of a *Chonopeltis* larva: stage I of *C. lisikili*. Most recently, Avenant-Oldewage & Knight (2008) provided updated distribution and prevalence data for *C. australis*, concluding that the species is actually limited to the Vaal river system, South Africa.

4.6. *Dolops*

Figs. 1B,D, 2H–I, 3E

The genus *Dolops* is a South-American genus with only two known exceptions: *D. ranarum* is found in sub-Saharan Africa and *D. tasmanianus* is found on Tasmania. The genus name is attributed to Audouin 1837 in a report on specimens of an unknown argulid (collected in Cayenne, French Guyana, from a *Hoplias aimara* (Characiformes) presented at a meeting in the Entomological Society of France. To Audouin the specimens had looked like *Argulus foliaceus* but lacking suction discs. He suggested a new genus *Dolops* (a name from Greek mythology, etymology uncertain), but the report was only published as a short note in the Bulletin of the Society (full account in Bouvier 1898). Heller was unaware of this publication as he proposed the genus called *Gyropeltis*, based on Branchiura collected in Brazil, again lacking suction discs (Heller 1857). However, Heller's (1857) investigation is the de-facto first treatment of the genus, with detailed drawings and descriptions. Krøyer (1863) as well as Thorell (1864) also used the name *Gyropeltis*. The latter even specifically mentioned that the description made by Audouin was insufficient (Thorell 1864). Bouvier took up the genus for new investigations 35 years later and concluded that Audouin's description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A1
A2
Mx1
Mc
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Thp1
Thp2
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Thp4
100 µm
B
1 µm
C
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A2
Mx1
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Thp1
Thp2
Thp3
Thp4
100 µm
E
A2
10 µm
F
10 µm
G
10 µm
H
Thp1
Thp2
Thp3
Thp4
100 µm
I
SLS
Mx1
10 µm

had been sufficiently detailed to be taxonomically valid (Bouvier 1897, 1898, 1899a,b). The works by Bouvier are still among the most detailed accounts available on South American *Dolops*.

Thiele (1904) provided an overview of the genus, while Maidl (1912) gave the first histological data on the integument, excretory and nervous systems of *D. longicauda*. His general conclusion was that *Dolops* and *Argulus* are very alike from an anatomical / histological point of view.

D. striata and *D. discoidalis* were collected in Paraguay and Brazil and described by Cunnington (1931) and Stekhoven (1937), but the taxonomy of the genus was not revised prior to the two works of Ringuelet (1943, 1948), in which a complete review of and dichotomous key to all the known South American species were given, later supplemented with new species described by Brian (1947) and Stekhoven (1951). *D. striata*, *D. geayi*, and *D. discoidalis* were collected in Venezuela by Weibezahn & Cobo (1964); *D. geayi* and *D. striata* again in the Brazillian Amazonas by Malta (1982) and Malta & Varella (1983), respectively, the latter also providing prevalence and collection data on *D. carvalhoi*. A new species, *D. intermedia*, was described from the Rio Grande do Sul region in Brazil by Silva (1978).

As apparent from the previous paragraph, data on the South American *Dolops* species is insufficient and scarce, and only a handful of recent publications are available, see Mamani et al. (2004), Nobre Carvalho et al. (2003) and references therein.

Most *Dolops* research has been conducted on the South African *Dolops ranarum*. Fryer contributed with the very important description of sperm transfer via spermatophores in several species of *Dolops*: *D. ranarum*, *D. geayi* and *D. discoidalis* (Fryer 1958, 1960b, 1969), leading him to include this property as a genus-characteristic trait (Fryer 1969). This assumption still has to be corroborated by further studies. The description of a new *Dolops* species from Tasmania, *Dolops tasmanianus* (Fryer 1969), could hint at a "Gondwanian" distribution of *Dolops* and this was also partly included in the discussion in the paper. Also, a closer affinity of *D. tasmanianus* to the South American species of *Dolops* was tentatively suggested (Fryer 1969). However, a closer look at current models for the Gondwana supercontinent still places Australasia (incl. Tasmania) very far away from the main distribution area of *Dolops*, i.e., central South America and Africa (see, e.g., Meert 2003). The distribution would then have to be explained by dispersal events, a few possibilities of which were also discussed by Fryer (1969).

Avenant et al. (1989a) made a complete redescription of *D. ranarum* (in fact, no detailed description had ever been published of the species), and Avenant et al. (1989b) contains the second ever published drawing of a *Dolops* larva. The morphology of the gut and digestive system of *D. ranarum* was described in detail in Avenant-Oldewage & van As (1990), while its feeding method when attached to a host catfish (*Clarias gariepinus*) and the injuries caused by this were described in Avenant-Oldewage (1994).

4.7. *Dipteropeltis*

Fig. 1E,F

The genus *Dipteropeltis* is monotypic with the species *Di. hirundo* described by Calman (1912). The material had been collected in the central part of Brazil some years earlier but had been mislabeled in the receiving museum collection (Calman 1912). Two other names were published for this material in 1913 and 1914, *Talaus riberoi* and *Moreiriella* according to Monod (1928), but they were considered junior synonyms of *Dipteropeltis* (Ringuelet 1943). The name *Talaus riberoi* is erroneously used by Yamaguti (1963) (see Fryer 1969 for corrections) and Overstreet et al. (1992) correctly considered it a junior synonym. In the two revisions of the Branchiura of Argentina, Ringuelet gave a detailed morphological description of *Dipteropeltis*, and presented new drawings of *Dipteropeltis* showing the cephalic appendages in better detail (Ringuelet 1943, 1948). A single picture of a *Dipteropeltis* specimen was given in Weibezahn & Cobo (1964), and the collection of a few specimens was mentioned recently in Nobre Carvalho et al. (2003) and Mamani et al. (2004). Only very few specimens of *Dipteropeltis* have ever been collected (approx. 25–30 in total) and very little is known about the genus, leaving many morphological and especially ecological and ontogenetic details unknown.

Fig. 2. Scanning electron micrographs. **A–C**: *Argulus foliaceus*. **A**: Oblique lateroventral view of adult. **B**: Detail of suction disc rim (distal part of second maxilla) in a juvenile, showing supporting sclerites. **C**: Close-up of pre-oral spine, not fully extended. **D–G**: *Chonopeltis australis*. **D**: Ventral view of male. **E**: Oblique lateroventral view of cephalic lobe of carapace showing support "rods" (arrows) (different specimen than D). **F**: Detail of second antenna from E. **G**: Detail of suction disc rim showing supporting sclerites. **H–I**: *Dolops ranarum*. **H**: Ventral view of thoracopods, adult. **I**: Midline view of first maxilla distal hook and seta-like structure.

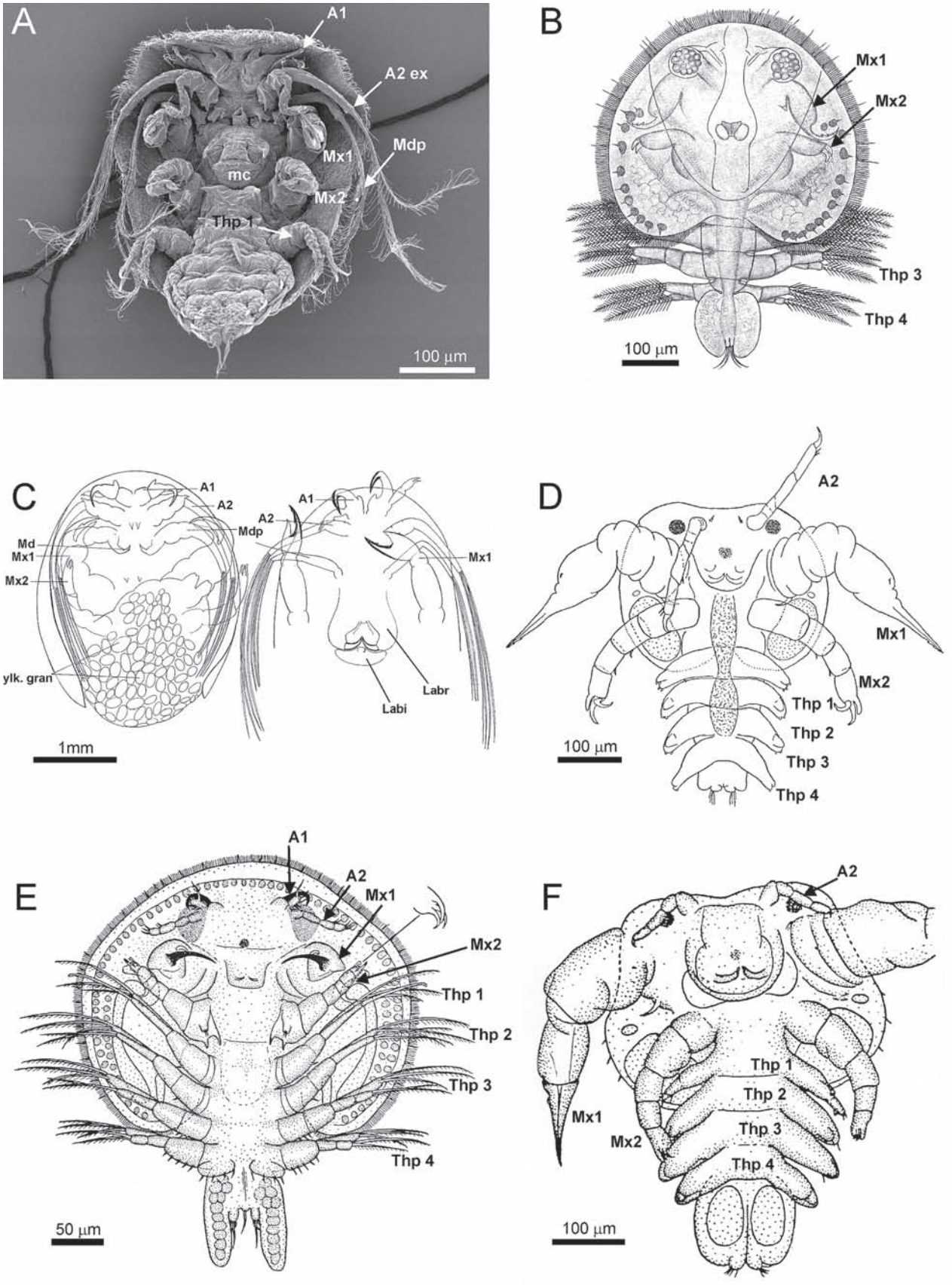

Fig. 3. A: *Argulus foliaceus*: Larval stage I, ventral view (SEM). **B**: *Argulus funduli*: Larval stage I, dorsal view. Reproduced with label modifications from Wilson (1907: pl. XXX). **C**: *Argulus viridis*: Late (29 days old) embryo (left), and detail of the anterior region of same (right). Reproduced with label modifications from Martin (1932: pl. II). **D**: *Chonopeltis inermis*: Larval stage I, ventral view. Reproduced with label modifications from Fryer (1956: fig. 77). **E**: *Dolops ranarum*: Larval stage I, ventral view. Reproduced with label modifications from Fryer (1964: fig. 24). **F**: *Chonopeltis brevis*: Larval stage II, ventral view. Reproduced with label modifications from Fryer (1961b: fig. 1).

5. Concluding remarks

The knowledge of Branchiura is patchy and inconsistent at best. A few species are known to a relatively high extent, especially *A. foliaceus*, *A. japonicus*, *A. coregoni*, and *D. ranarum*. As I have tried to document here, a fair knowledge of their morphology, ecology, and reproduction exists in the literature, probably due to the fact that these species are widespread in large parts of Europe and Asia, and *D. ranarum* is widespread in southern Africa. For most other species of *Argulus* and certainly all other species of *Dolops* such knowledge does not exist. The most intensively investigated *Chonopeltis* species are *C. inermis* and *C. australis*, but also for these species, the knowledge is far from extensive. Especially the apparent lethargic and inactive habitus of *Chonopeltis* adult as well as the larva's apparent inability to swim leaves many open questions on the precise life cycle of the genus: e.g., host finding and infection as well as mate finding and copulation. As shown above, the knowledge of *Dipteropeltis hirundo* is at a very rudimentary level, as material seems very difficult to obtain.

Even for the relatively well-known species, more questions than answers are found, and the list of unknowns given here is far from complete. With regard to the fundamental morphology, the nervous systems of *Dolops*, *Chonopeltis* and *Dipteropeltis* have not been described or depicted, and the descriptions of the *Argulus* nervous system contradict each other on important details. Only very rudimentary data can be found on the circulatory system of *Argulus*, while such data is missing completely for *Chonopeltis* and *Dolops*. The precise ontogeny and morphology of the complex mouth cone is still only understood at a rudimentary level, and only from observations on *Argulus* and *Chonopeltis*. In general, there is a severe lack of ontogenetic and embryological data on Branchiura; the larvae of no more than a handful of *Argulus* and *Chonopeltis* species are known, but so far there are no descriptions of *Dolops* larvae besides *D. ranarum*.

The lack of knowledge on Branchiura in general has also hampered any serious attempt at a morphology-based phylogenetic analysis of the genus. Often, the only source of information for most species is the original description and especially for *Dolops* (except *D. ranarum*) and *Dipteropeltis* this makes morphological comparisons difficult. The recent preliminary phylogenetic reconstruction mentioned above placed *Dolops* as the sister-group to the remaining Branchiura, but did not resolve the position of *Chonopeltis* adequately due to limited taxon sampling. Thus we are left with several open questions of the convergent or symplesiomorphic characters again underlining the need for further analyses of the Branchiura.

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8. Abbreviations

A1	First Antenna
A2	Second Antenna
Labr	Labrum
Labi	Labium
Mc	Mouth cone / proboscis
Md	Mandible
Mdp	Mandibular palp
Mx1	First Maxilla
Mx2	Second Maxilla
Sls	Seta-like structure
Thp1–4	First to fourth Thoracopod
ylk gran	yolk granules