

Redescription of *Axine belones* Abildgaard, 1794 (Monogenea, Axinidae), a gill parasite of *Belone belone* (Linnaeus, 1760) (Teleostei, Belonidae) off the Algerian coast, Western Mediterranean

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Abstract: *Axine belones* Abildgaard, 1794 is a polyopisthocotylean monogenean, parasite of belonid fishes, and there are few accounts with morphological and morphometrical data. Here, we redescribe *A. belones* based on newly collected specimens from its type-host, the garfish *Belone belone* (Linnaeus, 1760) collected off Algeria, Western Mediterranean, a new locality for this species. Several anatomical and morphological features (genital apertures and clamps sclerites) are described and illustrated. We provide morpho-anatomical and morphometrical data, along with detailed illustrations of *A. belones*, and we discuss the host specificity of *A. belones*. Notes on hosts and localities of this species and other congeners are presented, and host specificity patterns of *A. belones* revealed stenoxenic specificity to *Belonidae* Bonaparte, 1835, whilst the genus *Axine* Abildgaard, 1794 seems to be restricted to fishes of the order Beloniformes. Our attempt to investigate morphometric variations between Mediterranean and oceanic specimens revealed that the two populations differed by the number of testes, body length, and clamp dimensions. However, the limited number of measured organs in the various accounts precluded any distinction between the populations. Molecular data for both Mediterranean and oceanic specimens are needed to determine the existence of cryptic species.

Keywords: Polyopisthocotylea; taxonomy; morpho-anatomical; host specificity; cryptic species

Sažetak: PONOVI OPIS NAMETNIKA *AXINE BELONES* ABILDGAARD, 1794 (MONOGENEA, AXINIDAE), PRONAĐENOG NA ŠKRGAMA IGLICE *BELONE BELONE* (LINNAEUS, 1760) (TELEOSTEI, BELONIDAE) UZ ALŽIRSKU OBALU U ZAPADNOM SREDOZEMNOM MORU. *Axine belones* Abildgaard, 1794 je jednorodni metilj, nametnik na škrigama iglice, o kojem postoji malo radova s morfološkim i morfometrijskim podacima. U ovom radu dajemo ponovni opis vrste *A. belones* na temelju primjeraka sakupljenih na iglici *Belone belone* (Linnaeus, 1760), njegovog tipskog domaćina. Primjerci iglica su ulovljeni uz obale Alžira, u zapadnom Sredozemnom moru, što je ujedno i novi lokalitet za ovu vrstu nametnika. Opisano je i ilustrirano nekoliko anatomskih i morfoloških značajki (genitalni otvori i skleriti prijanjaljki). U radu se iznose morfo-anatomske i morfometrijske podatke, zajedno s detaljnim ilustracijama *A. belones* i raspravlja o specifičnosti domaćina *A. belones*. Prikazani su i zabilježeni domaćini i lokaliteti nalaza ove vrste i srodnika, a obrasci specifičnosti domaćina kod *A. belones* ukazali su na stenoksičnu specifičnost prema porodici *Belonidae* Bonaparte, 1835, dok je rod *Axine* Abildgaard, 1794 vjerojatno ograničen na ribe reda Beloniformes. Naš pokušaj da istražimo morfometrijske varijacije između sredozemnih i oceanskih jedinki otkrio je da se dvije populacije razlikuju po broju testisa, duljini tijela i dimenzijama prijanjaljki. Međutim, ograničeni broj izmjerenih organa u drugim literaturnim izvorima onemogućio je precizno utvrđivanje razlike između populacija. Postojanje kriptičnih vrsta bi se moglo dokazati korištenjem molekularnih metoda za sredozemne i oceanske uzorke.

Ključne riječi: Polyopisthocotylea; taksonomija; morfo-anatomske; specifičnost domaćina; kriptične vrste

INTRODUCTION

The family Axinidae Monticelli, 1903 was proposed by Unnithan (1957) to accommodate *Axine* Abildgaard, 1794 and its related genera. These genera were previously placed under the subfamily Axininae Monticelli, 1903 within the family Microcotylidae Taschenberg, 1879, as mentioned by Sproston (1946), Hargis (1956), Unnithan

(1957), and Price (1962). The latter, not only provided classification keys for subfamilies and genera but also provided revised descriptions and illustrations for several species (Price, 1962).

Members of Axinidae are characterised by the triangular shape of the haptor, persistence of larval anchors or hooks in adult worms, and their J-shaped ovary (Price, 1962). They somewhat resemble certain

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Table 1. Hosts and localities of *Axine* spp. Note that except for *Chelidonichthys lucerna* (Linnaeus, 1758) (Scorpaeniformes), all hosts are members of Beloniformes. Abbreviations: E, Eastern; EC, Eastern Central; NE, Northeast; NW, Northwest; SE, Southeast; WC, Western Central. ¹See discussion.

Parasite	Type-host	Family of type-host	Type locality	Reference
<i>Axine belones</i> Abildgaard, 1794	<i>Belone belone</i>	Belonidae	NE Atlantic, off Denmark	Abildgaard (1794)
<i>Axine buccina</i> Kritsky and Bakenhaster, 2022	<i>Hyporhamphus unifasciatus</i>	Hemiramphidae	WC Atlantic, Gulf of Mexico	Kritsky and Bakenhaster (2022)
<i>Axine cypseluri</i> (Meserve, 1938) ¹	<i>Cypselurus collopterus</i>	Exocoetidae	SE Pacific, Galápagos Islands	Meserve (1938)
<i>Axine depauperati</i> Yamaguti, 1968	<i>Hemiramphus depauperatus</i>	Hemiramphidae	EC Pacific, off Hawaii	Yamaguti (1968)
<i>Axine hemirhamphae</i> Tripathi, 1959	<i>Hemiramphus depauperatus</i>	Hemiramphidae	E Indian ocean, off India	Tripathi (1959 (1957))
<i>Axine hemiramphae</i> Unnithan, 1957	<i>Rhynchorhamphus georgii</i>	Hemiramphidae	E Indian ocean, off India	Unnithan (1957)
<i>Axine hyporhampi</i> Price, 1962	<i>Hyporhamphus</i> sp.	Hemiramphidae	NW Atlantic, off Massachusetts	Price (1962)
<i>Axine ibanezi</i> Tantaleán, 1975	<i>Exocoetus volitans</i>	Exocoetidae	SE Pacific, off Peru	Tantaleán (1974)
<i>Axine inada</i> Ishii and Sawada, 1938	<i>Seriola quinqueradiata</i>	Carangidae	NW Pacific, off Japan	Ishii and Sawada (1938)
<i>Axine japonica</i> Price, 1946	<i>Cheilopogon agoo</i>	Exocoetidae	NW Pacific, off Japan	Yamaguti (1963)
<i>Axine parini</i> Gichenok, 1974	<i>Euleptorhamphus viridis</i>	Hemiramphidae	Indian Ocean, Pacific Ocean	Gichenok (1977)
<i>Axine spilonotopteri</i> Yamaguti, 1968	<i>Cheilopogon spilonotopterus</i>	Exocoetidae	EC Pacific, off Hawaii	Yamaguti (1968)
<i>Axine triglae</i> Van Beneden and Hesse, 1863	<i>Chelidonichthys lucerna</i>	Triglidae	NE Atlantic, off Brest	Van Beneden and Hesse (1863)
<i>Axine yamagutii</i> (Meserve, 1938)	Unidentified flying-fish	Likely Exocoetidae	EC Pacific, off Mexico	Meserve (1938)

Gastrocotylidae Price, 1943 such as *Pseudaxine* Parona and Perugia 1890 in their body shape, but they are widely separated especially by body dimensions, and the organisation of their genital atrium and terminal lappet.

The Axinidae currently comprise 15 genera (WoRMS, 2023a). The most speciose genera are the genus *Axine* and the genus *Axinoides* Yamaguti, 1938. The type-genus of this family was erected in 1794 by Abildgaard with the type species *Axine belones* Abildgaard, 1794 from *Belone belone* (Linnaeus, 1760) (as *Belone acus* Risso, 1827) (Abildgaard, 1794). Currently, *Axine* contains 14 species (WoRMS, 2023b) (Table 1). Among these species, *A. belones*, first described from the North East Atlantic, off Denmark is the sole inhabiting the Mediterranean (Table 2), while the other species are found in the Atlantic (Van Beneden and Hesse, 1863; Price, 1962; Kritsky and Bakenhaster, 2022); Pacific (Ishii and Sawada, 1938; Meserve, 1938; Yamaguti, 1963; Yamaguti, 1968; Tantaleán, 1974) and Indian Oceans (Tripathi, 1959 (1957); Unnithan, 1957; Gichenok, 1977).

In an ongoing survey on polyopisthocotylean parasites of marine teleosts off the Algerian coast

(Bouguerche *et al.*, 2019a, 2019b, 2019c, Derouiche *et al.*, 2019; Bouguerche *et al.*, 2020a, 2020b; Azizi *et al.*, 2021; Bouguerche *et al.*, 2021a, 2021b; Ayadi *et al.*, 2022; Gastineau *et al.*, 2023), we recovered several polyopisthocotyleans of the garfish *B. belone*. There are no previous studies of monogeneans on belonid fishes in Algerian waters. In addition, morphometrical data and details on the internal anatomy and clamps were not provided in the original description, and the only available redescription of this species is that of Châari *et al.* (2016), who unfortunately provided no new illustrations. In this paper, we redescribe this species and provide detailed morpho-anatomical and morphometrical data, along with illustrations.

MATERIAL AND METHODS

Fish sampling and examination

Between June 2017 and September 2018, a total of 69 specimens of *B. belone* were collected from local fishermen in two regions off the Algerian coast: from Bouharoun (36°37'24"N, 2°39'17"E) and Cap Djinet (36°52'37"N, 3°43'23"E). The collected fish specimens were transferred immediately to the

Table 2. Hosts and localities of *Axine belones*. Abbreviations: C, Central; W, Western; E, Eastern; NE, North-Eastern.

Hosts and their locality records	References
<i>Belone belone</i> (type-host)	
Northeast Atlantic, off Denmark,	Abildgaard (1794)
W Mediterranean, off France, Spain	Euzet and Lopez-Roman (1973)
C Mediterranean, off Italy	Parona (1902); Palombi (1949); Ulmer and James (1981)
E Mediterranean, off Turkey	Özer and Yurakhno (2013)
C Mediterranean, off Montenegro	Radujkovic and Euzet (1989)
W Mediterranean, off Tunisia	Euzet and Lopez-Roman (1973); Châari <i>et al.</i> (2015); Châari <i>et al.</i> (2016)
W Mediterranean, off Algeria	Present study
NE Atlantic, off Brest, Plymouth, and North Sea	Dawes (1968)
NE Atlantic, off France	van Beneden (1856) in Radujkovic and Euzet (1989)
NE Atlantic, off UK	Scott (1911)
NE Atlantic, Baltic Sea, off Germany	Dawes (1968); Unger <i>et al.</i> (2018)
Black sea, off Russia	Strelkov (1964)
<i>Belone senegalensis</i>	
Atlantic	Baer (1972)

laboratory (LEBEIG, USTHB) and identified using Fischer *et al.* (1987). The gills were removed, placed in separate Petri dishes containing seawater, and observed under a stereomicroscope (Carl Zeiss™ Stemi™ DV4 Stereomicroscope, Germany) for the presence of monogeneans. Synonyms, common and scientific and common names of fishes are those provided in WoRMS and FishBase, respectively (Froese and Pauly, 2023).

Monogenean collection and morphological study

Monogeneans were removed alive from gills using fine dissection needles, heat-killed with boiling water then preserved in 70% ethanol. Some specimens were stained with acetic carmine, dehydrated in ethanol series (70, 96, and 100%), cleared in clove oil, and finally mounted in Canada balsam to analyse the internal organs (Justine *et al.*, 2013). Other specimens were mounted in Berlese fluid to study the morphology of clamps and spines of the genital atrium. Slides of monogeneans were deposited in the SMNH, under registration numbers SMNH 220248 – 220262.

Whole stained mounts were photographed using a Zeiss microscope equipped with a camera. Drawings were made with the help of a microscope equipped with a drawing tube (Leitz Microscope, Wetzlar, Germany). Drawings were scanned and redrawn on a computer with Adobe Illustrator (CS5, Adobe Systems, San Jose, CA, USA). Nomenclature of clamps sclerites follows Euzet and Lopez-Roman (1973). Nomenclature of sclerotised pieces at level of haptor (anchors and *crochets en fléau* follows Kritsky and Bakenhaster (2022). Measurements

of clamps were made following Villora-Montero *et al.* (2020). The sclerotised structures of the haptor (anchors and hooks) were measured according to Fig. 1. Measurements of body parts follows Châari *et al.* (2016) and are in micrometers, and indicated as means, and in parentheses, the range and number of measurements.

RESULTS

Axine belones Abildgaard, 1794

Synonyms: *Heteracanthus pedatus* Diesing, 1836; *Heteracanthus sagittatus* Diesing, 1836; *Axine orphii* Beneden and Hesse, 1863; *Axine platyura* Creplin, 1838 (Price, 1962).

Type-host: *Belone belone* (as *Belone acus*) (Abildgaard, 1794).

Other hosts: *Strongylura senegalensis* (Valenciennes, 1846) (as *B. senegalensis* Valenciennes, 1846 (Baer, 1972)). *Tylosurus imperialis* (Rafinesque, 1810) (Palombi, 1949). *Cheilopogon heterurus* (Rafinesque, 1810) (*Exocoetus heterurus* Rafinesque, 1810) (Palombi, 1949). *Exocoetus volitans* Linnaeus, 1758 (Palombi, 1949). *Hirundichthys rondeletii* (Valenciennes, 1847) (*Exocoetus rondeletii* Valenciennes, 1847) (Palombi, 1949).

Type-locality: off Denmark, Northeast Atlantic (Abildgaard, 1794).

Site on host: Gills.

Specimens from Algeria: Vouchers deposited in the collections of the Swedish Museum of Natural History, Stockholm (SMNH 220248 – 220262).

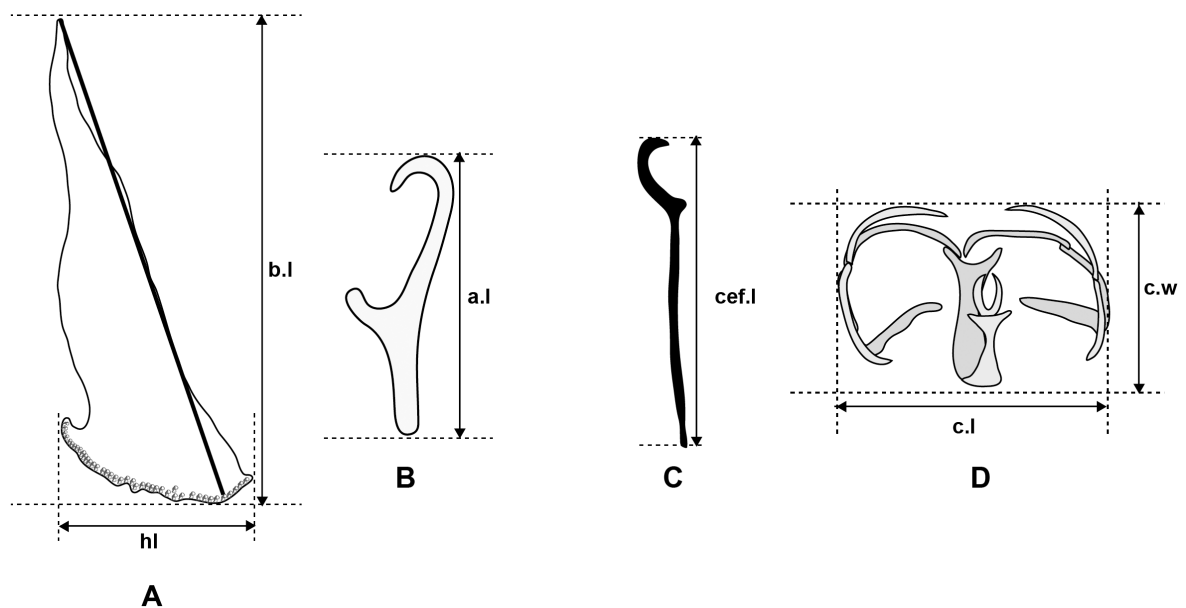


Fig. 1. Schematic drawings for measurements (SMNH 220251). Body outline for body length, haptor length and number of clamps (A); Anchor length (B); *Crochet en fléau* (C); Clamp measurements (D); c.l.: clamp length, c.w.: clamp width. Measurements follow Villora-Montero et al. (2020). Abbreviations: b.l., body length; a.l., anchor length; cef.l., *Crochet en fléau* length; c.l., clamp length; c.w., clamp width.

REDESCRIPTION

Comparative measurements are indicated in Table 3. Body triangular, narrowed anteriorly (Fig. 2 A) 4769 μm (2225–5700 μm , $n = 21$) long by 533 μm (320–780 μm , $n = 21$) wide at level of ovary. Haptor asymmetrical, oblique, 1705 μm (900–2150 μm , $n = 21$) long, consisting of a single long row of 52 (44–60, $n = 20$) clamps situated along posterior edge of body; anchor bearing lobe minute, embedded in the tegument, barely visible in most specimens, not delimited from haptor, situated among the clamps; lobe bearing 2 pairs of anchors. Ten of 24 specimens with haptor directed to right and with clamps situated on same side of genito-intestinal canal; six specimens with haptor pointed to left, clamps located on the opposite genito-intestinal canal side. Genito-intestinal canal not observed on the remaining specimens. Number of clamps at right side of anchors and *crochets en fléau* 30 (22–38, $n = 8$), at left side 21 (17–23, $n = 8$). Clamps 48 (40–55, $n = 18$) long by 85 (72–100, $n = 18$) wide, “*Axine* type” (Fig. 2 F), formed by two jaws, with marginal sclerites of anterior and posterior jaw, in two parts.

Anterior jaw with long median sclerite; distal end of median sclerite T-shaped with two short branches; median sclerite continued with a widened and curved part. Anterior jaw supported by two peripheral sclerites: two lateral sclerites and two axial sclerites (Fig. 3 A). In posterior jaw, median sclerite shorter than in anterior jaw, T-shaped. Two V-shaped sclerotised pieces articulated distally on median sclerite. On proximal side, lateral sclerite and axial sclerite continued each in posterior jaw by visible extensions that do not reach sclerotised pieces. Posterior jaw also supported by peripheral sclerites: two lateral sclerites and two axial

sclerites. Peripheral sclerites articulated proximally (Fig. 3 B). On proximal side, muscle connecting both jaws (Fig. 3 C). Haptoral lappet small, embedded generally in middle of haptor, armed with one pair of anchors and one pair of *crochet en fléau* (Fig. 2 E). Anchors and *crochets en fléau* situated at 298–385 (390) ($n = 14$) from posterior end of haptor.

Oral suckers subcircular, aseptate (Fig. 2 B), 30 μm (16–42, $n = 20$) long by 39 μm (28–48, $n = 20$) wide. Pharynx oval, muscular, 36 μm (26–46, $n = 20$) long by 29 (20–42, $n = 20$) wide, continued by long oesophagus. Oesophagus divided in two intestinal branches (Fig. 4); left intestinal branch slightly longer. Intestinal branches with lateral diverticula and extending into haptor.

Testes 42–58 in number, located in intercaecal field of posterior half of body, arranged in two longitudinal rows and posteriorly in single row. Vas deferens ventral, winding, extending to base of male copulatory organ.

Cirrus muscular and conical, armed at its base with one basal row of 23 (20–27, $n = 5$) thorns (Fig. 5). Genital atrium ventral, located at 499 μm (510–920, $n = 19$) from anterior end, opening mid-longitudinally. Genital atrium armed with three groups of spines: median group formed of 12 (10–14, $n = 13$) thorns arranged in single crown; two lateral groups of 20 (13–24, $n = 13$) thorns, symmetrical to longitudinal axis of cirrus and located on either side of the crown. Groups of spines supported by a visible muscle base (Fig. 6).

Ovary J-shaped, distal limb pre-testicular (Fig. 7). Proximal limb longer than distal limb. Oviduct long, extending to midline where it receives the genito-intestinal canal. Genito-intestinal canal flowing into left intestinal branch. Ovovitelline duct fairly long. Oötype large, fusiform; Mehlis glands at bases of oötype.

Vagina complex (Fig. 4), located at 993 μm (685–

Table 3. Measurements of *Axine belones* from *Belone belone* from various localities. Measurements of body parts are in micrometers, and indicated as means, and in parentheses, the range and number of measurements.

Locality	Plymouth, Atlantic	Black Sea	Montenegro, northern Mediterranean	France, Tunisia, Spain, Mediterranean	Tunisia, southern Mediterranean	Algeria, southern Mediterranean
Reference	Price (1962)	Strelkov (1964)	Radujkovic and Euzet (1989)	Euzet and Lopez-Roman (1973)	Châari <i>et al.</i> (2016)	Present study
Number of measured specimens	3	60	3	125	18	26
Body length	4400-8000	4000-6000	4000-9000	5600-9700	5400 (3900-7250)	4769 (2225-5700, n = 21)
Haptor length	1700				1520 (1150-2000)	1705 (900-2150, n = 21)
Body width		1000-1500	1800-2000	1440-2230	680 (400-1050)	533 (320-780, n = 21)
Clamp number	60-65	28-54	50-70	68 (59-77)	60 (43-66)	52 (44-60, n = 20)
Clamp length	95-115	110-113			87 (70-110)	85 (72-100, n = 18)
Clamp width		70-80			20-60	48 (40-55, n = 18)
<i>Crochet en fléau</i> length	40					33 (30-36, n = 14)
Anchor length	50					42 (38-50, n = 7)
Oral suckers length	57		40	47-49	36 (30-40)	30 (16-42, n = 20)
Oral suckers width			30	30-33	27 (20-35)	39 (28-48, n = 20)
Pharynx length	30			39-42		36 (26-46, n = 20)
Pharynx width	20			27-30		29 (20-42, n = 20)
Distance genital atrium-anterior end				600-1200		499 (510-920, n = 19)
Spines of genital atrium						
Two lateral groups (Number)						20 (13-24, n = 13)
Two lateral groups (Length)				20-28	13 (10-19)	15 (14-16, n = 13)
Median (Number)						12 (10-14, n = 13)
Median (Length)				10-12	10 (8-12)	15 (14-15, n = 13)
Posterior crown (Number)						23 (20-27, n = 13)
Posterior crown (Length)				17-24	16 (14-22)	15 (14-16, n = 13)
Number of testes	60		18-20	40-50	30-41	47 (33-65, n = 13)
Distance vagina - anterior end						993 (685-1230, n = 19)
Vagina length						44 (36-60, n = 20)

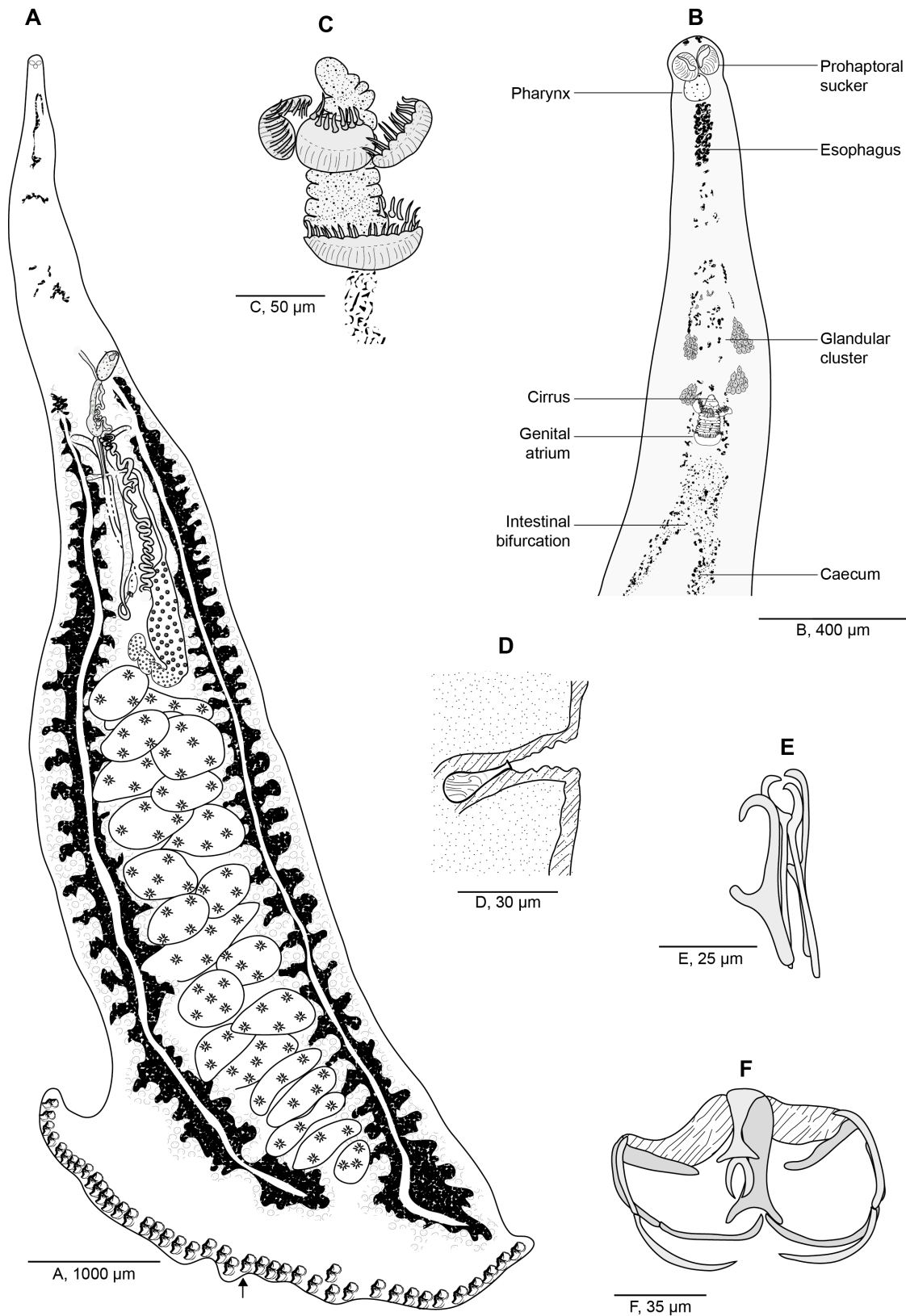


Fig. 2. *Axine belones* Abildgaard, 1794 from *Belone belone*. Whole body, dorsal view (SMNH 220251) (A); Anterior part showing relative positions of intestinal bifurcation and position of male copulatory organ, ventral view (SMNH 220256) (B); Male copulatory organ, ventral view (SMNH 220250) (C); Vagina, dorsal view (SMNH 220250) (D); Anchor and *crochet en fléau* of terminal lappet (SMNH 220251) (E); Clamp, dorsal view (SMNH 220251) (F). Position of the terminal lappet in body indicated by an arrow.

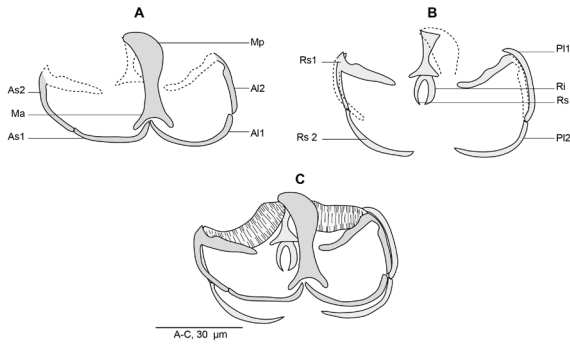


Fig. 3. *Axine belones* from *Belone belone* (SMNH 220251). Ventral jaw (A); Dorsal jaw (B); Clamp, ventral view (C); Ma, median sclerite. Mp, curved part (distal end) of median sclerite. Al1-2, lateral peripheral sclerites of anterior jaw. As1-2, axial peripheral sclerites of anterior jaw. Pl1-2, lateral peripheral sclerites of posterior jaw. Rs1-2, axial peripheral sclerites of posterior jaw. Rs-Ri, V-shaped sclerotised pieces.

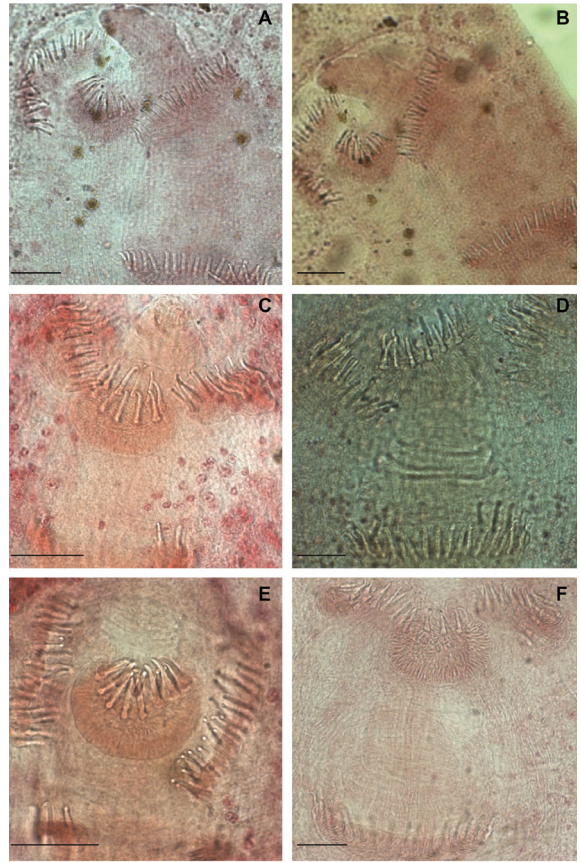


Fig. 5. *Axine belones* from *Belone belone*. Arrangements of spines of the male copulatory organ and of the cirrus, ventral view. Scale: 20 µm. SMNH 220262 (A, B); SMNH 220255 (C); SMNH 220258 (D); SMNH 220255 (E); SMNH 220248 (F).

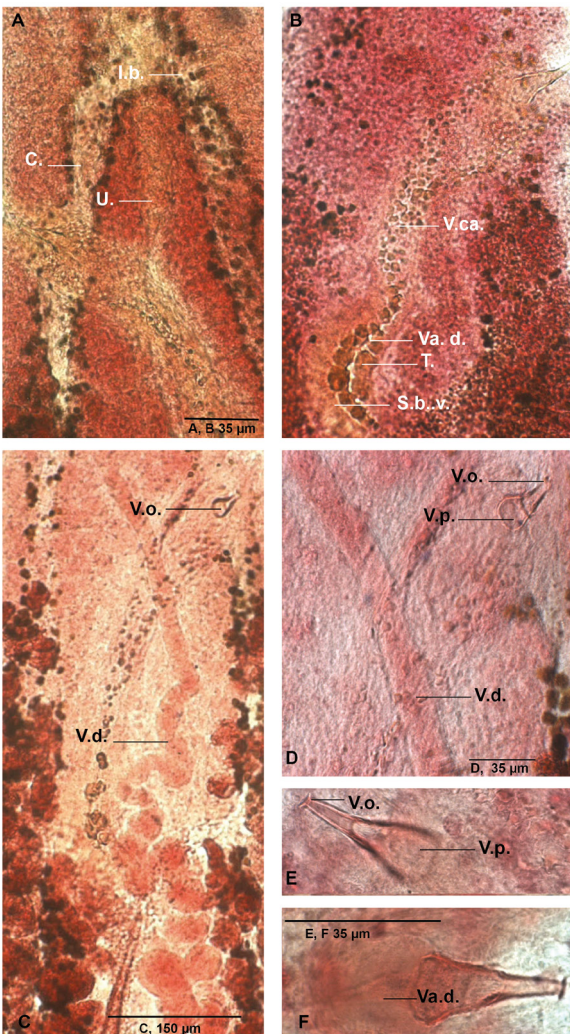


Fig. 4. *Axine belones* from *Belone belone*. Detailed anatomy of reproductive organs in the region of the vagina (SMNH 220251). Anterior part, ventral view (A); Vagina, dorsal view (B-F). Abbreviations: l.b, intestinal bifurcation; C., caeca; U., uterus; V.ca, vaginal cavity; Va.d, vaginal duct; T, thorns; S.b.v, sclerotised base of vagina; V.o, vaginal opening; V.d, vas deferens.

1230, n = 19) from anterior end, immediately posterior to intestinal bifurcation, opening laterally (Fig. 2 D). Vaginal aperture with large vaginal cavity, 44µm (36–60, n = 20) long; walls of vaginal cavity covered with small thorns (Fig. 8). Vaginal cavity ending in a concave muscular base provided with numerous irregular sclerotised structures. Vitellarium lateral, surrounding intestinal branches and extending from vaginal pore to haptor. Transverse vitelloducts uniting slightly at base of the muscular part of vaginal canal forming common vitelline duct. Eggs not observed.

Differential diagnosis

By their morpho-anatomical characters, our specimens of *A. belones* are similar to those presented in previous redescrptions of this species available in the literature (Price, 1962; Euzet and Lopez-Roman, 1973). Morpho-anatomical details of our specimens agree with those provided previously, especially in respect of presence of haptor hooks in minute lappet. A lappet armed with three hooks was mentioned in all previous descriptions of this species (Price, 1962; Euzet and Lopez-Roman, 1973), except in Sproston (1946) who beautifully illustrated this species, but failed to observe or to illustrate the slender minute hooks (Sproston, 1946; Price, 1962;).

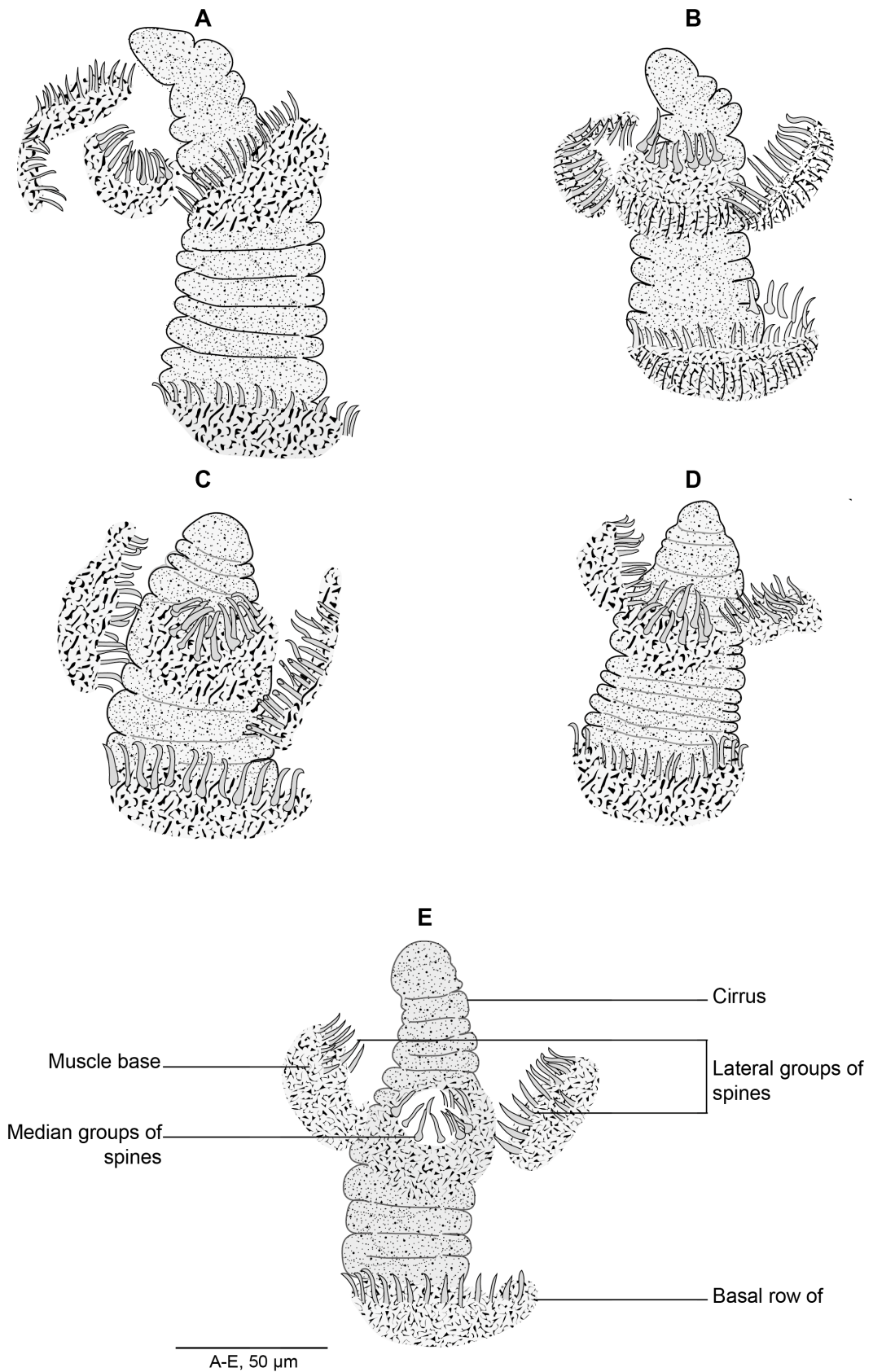


Fig. 6. *Axine belones* from *Belone belone*. Arrangements of spines of the male copulatory organ, ventral view. Note that the arrangement shown in Figure 6 (A) is a deformed position. SMNH 220262 (A); SMNH 220258 (B); SMNH 220255 (C – E).

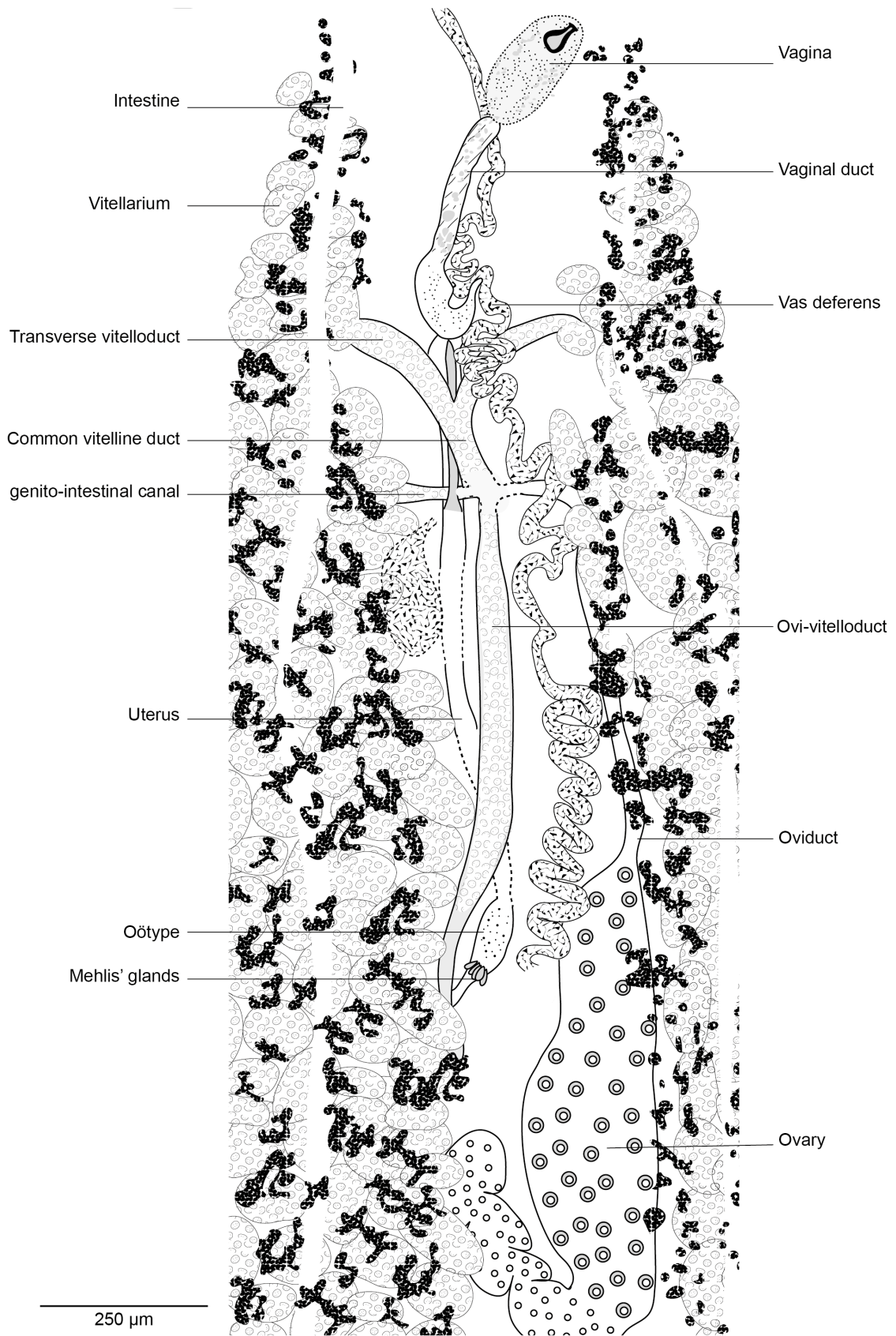


Fig. 7. *Axine belones* from *Belone belone*. Detailed anatomy of reproductive organs in the region of the ovary, dorsal view (SMNH 220251).

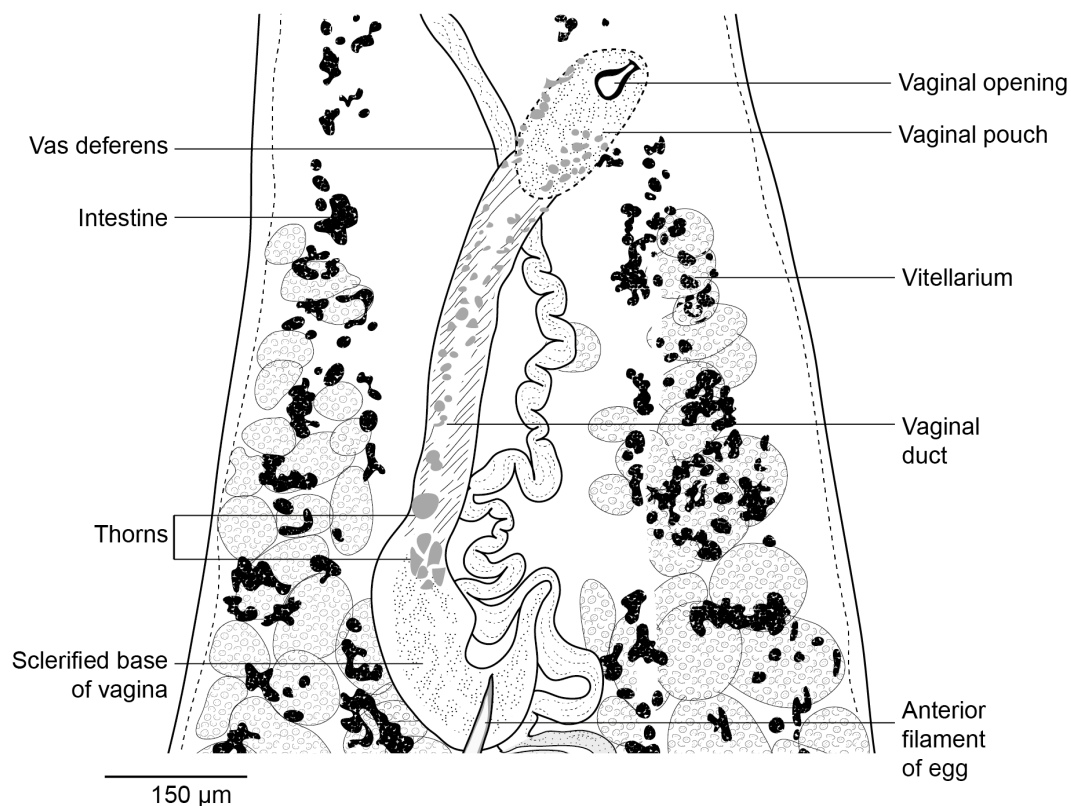


Fig. 8. *Axine belones* from *Belone belone*. Detailed anatomy of reproductive systems in the region of the vagina, dorsal view (SMNH 220251).

We attempted to compare Mediterranean specimens with those from the Atlantic Ocean (Table 3). Specimens of *A. belones* collected off Algeria differ from the Mediterranean specimens from the same host off Tunisia in having a slightly smaller body (2225–5700 × 320–780 vs. 3900–7250 × 400–1050), longer haptor (900–2150 vs. 1150–2000), and more numerous testes (33–65 vs. 30–41). Other measurements, such as dimensions of clamps, dimensions of oral suckers, and number of spines of genital atrium overlap. Specimens from Algeria differed from those described by Euzet and Lopez-Roman (1973) only by a smaller body (2225–5700 × 320–780 μm vs. 5600–9700 × 1440–2230 μm), fewer clamps (44–60 vs. 59–77), more testes (33–65 vs. 40–50), and smaller oral suckers (16–42 × 28–48 μm vs. 47–49 × 30–33 μm). They also differ by the number of spines of the genital atrium, mainly of lateral groups, and the posterior crowns are also more numerous in specimens described by Euzet and Lopez-Roman (1973). Our specimens could also be distinguished from those collected off Montenegro by having a smaller body (2225–5700 × 320–780 μm), fewer clamps (44–60 vs. 50–70), and more testes (33–65 vs. 18–20).

Only a few measurements are available for comparison with specimens reported from the Black Sea by Strelkov (1964), since the author provided only body dimensions and clamp number, length and width. The specimens of *A. belones* collected off Algeria can also be distinguished from the Atlantic specimens (Plymouth)

described from the same host by Price (1962) in having a slightly smaller body (2225–5700 vs. 4400–8000 μm). However, we note that measurements given by Price (1962) were based upon only 3 specimens collected separately on September 30, 1932 (1 specimen) and December 10, 1933 (2 specimens), respectively at Plymouth, England, by Hon. Miriam Rothschild.

Overall, specimens off Montenegro (Radujkovic and Euzet, 1989) appear to have fewer testes (18–20 vs. 40–50 (Euzet and Lopez-Roman, 1973); vs. 30–41 (Châari *et al.*, 2016). However, the length of Montenegrin specimens falls within the range of other Mediterranean specimens. Specimens from the Black Sea differ from the Mediterranean specimens (Châari *et al.*, 2016) only by having slightly wider clamps (70–80 vs. 20–60 μm), whereas specimens from the Atlantic (Price, 1962) could be distinguished from the Mediterranean specimens by having more testes (Table 3).

Unfortunately, few measurements are available for comparison and the measured organs differed from one account to another, precluding further comparison between the Mediterranean and oceanic specimens. It is likely that different cryptic species are involved, but this suggestion is premature in light of the data available so far.

DISCUSSION

Overall, the genus *Axine* is characterised by a narrow host range and a wide geographical distribution. *Axine* spp. have been reported from the Atlantic (Van Beneden and Hesse, 1863; Price, 1962; Strelkov, 1964), Indian (Price, 1962) and Pacific Oceans (Yamaguti, 1968; Tantaleán, 1974). Only *A. belones* occurs in the Mediterranean and remains a poorly known species. The first exhaustive data on adult morphoanatomy are those from Euzet and Lopez-Roman (1973). The last redescription of the species is that of Châari *et al.* (2016) who generally followed Euzet and Lopez-Roman (1973) without providing further morpho-anatomical precisions.

With respect to host specificity, this genus comprises mostly gill polyopisthocotyleans parasites of Belonidae (Strelkov, 1964; Yamaguti, 1968), Hemiramphidae Gill, 1859 (Price, 1962; Yamaguti, 1968) and Exocoetidae Risso, 1827 (Yamaguti, 1968; Tantaleán, 1974), all members of the Beloniformes (Froese and Pauly, 2023). A single species, *Axine triglae* Van Beneden and Hess, 1863, is known from a non-Beloniformes host, *Chelidonichthys lucerna* (Linnaeus, 1758) (Scorpaeniformes, Triglidae Rafinesque, 1815) (Van Beneden and Hesse, 1863). There is a single mention of *A. belones* on *Strongylura senegalensis* (as *B. senegalensis*) in a checklist (Baer, 1972), without morphological details nor morphometric data to justify the assignment of this monogenean to *A. belones*. This record needs to be confirmed.

The host specificity pattern of *A. belones* is fairly comparable to that of congeneric species, as most *Axine* spp. occur in beloniform hosts (Table 1). However, based on the available host records of this species, we note that *A. belones* exhibits stricter host specificity. This member of the Axinidae has been reported from the Mediterranean (Euzet and Lopez-Roman, 1973; Radujkovic and Euzet, 1989; Châari *et al.*, 2016), the Black Sea (Strelkov, 1964), and the Atlantic Ocean (Price, 1962) from a single host species, *B. belone* (Table 2), which advocates for oixenic specificity for this polyopisthocotylean, like several axinids. In this sense, the genus *Axine* seems to be restricted to fishes of the order Beloniformes, whereas *A. belones* is host-specific to *B. belone*. Yet, this oioxenic specificity is not unusual in Axinidae. In fact, the different subspecies of agujon needlefish: *Tylosurus acus* (Lacepède, 1803), also member of the family of Belonidae each harbour their own Axinidae, in their respective distribution areas (Châari *et al.*, 2010). We note however, that according to Froese and Pauly (2023), the 3 subspecies of *T. acus* were upraised at species rank as provisionally accepted names, until more works are conducted on the 3 subspecies to fix their status. The corresponding monogenean Axinidae are *Nudaciraxine imperium*

Châari, Derbel and Neifar, 2010, *Neoaxine constricta* (Yamaguti, 1938) and *Nudaciraxine gracilis* (Linton, 1940). Their hosts and localities are as follows:

- *Nudaciraxine imperium* parasitises the Mediterranean species *Tylosurus imperialis* (Rafinesque, 1810) (Châari *et al.*, 2010).
- *Neoaxine constricta* (Yamaguti, 1938) parasitises in the Pacific Ocean species *Tylosurus melanotus* (Bleeker, 1850) (Yamaguti, 1938; Price, 1945).
- *Nudaciraxine gracilis* (Linton, 1940) parasitises the Atlantic species *Tylosurus acus* (Lacepède, 1803) (Linton, 1940; Price, 1962; Châari *et al.*, 2010).

In addition, Baer (1972) listed *A. belones* on the tropical two-wing flying fish *Exocoetus volitans* Linnaeus, 1758, which is a ray-finned fish (Exocoetidae) in the order Beloniformes (Froese and Pauly, 2023), in the Indian Ocean in his checklist, with no description nor morphometric data. This record needs to be confirmed; it could be that the species involved was *Axine ibanezi* Tantaleán, 1975, described from this host.

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