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Ultrastructural study of the jaw structures in two species of Ampharetidae (Annelida: Polychaeta)

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Abstract

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Two species of jaw bearing Ampharetidae (*Adercodon pleijeli* (Mackie 1994) and *Ampharete* sp. B) were investigated in order to describe the microanatomy of the mouth parts and especially jaws of these enigmatic polychaetes. The animals of both studied species have 14–18 mouth tentacles that are about 30 μm in diameter each. In both species, the ventral pharyngeal organ is well developed and situated on the ventral side of the buccal cavity. It is composed of a ventral muscle bulb and investing muscles. The bulb consists of posterior and anterior parts separated by a deep median transversal groove. In both species, the triangular teeth or denticles are arranged in a single transversal row on the surface of the posterior part of the ventral bulb just in front of its posterior edge. There are 36 denticles in *Adercodon pleijeli* and 50 in *Ampharete* sp. B. The height of the denticles (6–12 μm) is similar in both species. Each tooth is composed of two main layers. The outer one (dental) is the electron-dense sclerotized layer that covers the tooth. The inner one consists of long microvilli with a collagen matrix between them. The thickness of the dental layer ranges from 0.95 to 0.6 μm. The jaws of the studied worms may play a certain role in scraping off microfouling. The fine structure of the jaws in Ampharetidae is very similar to that of the mandibles of Dorvilleidae, the mandibles and the maxillae of Lumbrineridae, Eunicidae and Onuphidae, and the jaws of other Aciculata. This type of jaw is characterized by unlimited growth and the absence of replacement. The occurrence of jaws in a few smaller Ampharetidae is considered as an apomorphic state.

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Introduction

In polychaetes a muscular pharynx armoured by jaws has traditionally been considered to be typical for Phyllodocida and Eunicida (Ushakov 1955; Fauchald and Rouse 1997; Tzetlin and Purschke 2004), recently named Aciculata (Rouse and Fauchald 1997; Rouse and Pleijel 2001). Jaw-like structures are found in polychaetes with an axial muscular proboscis (AMP) as well as in some with a ventral pharyngeal organ (VPHO) (Wolf 1980; Purschke 1987). While an axial muscular proboscides occurs only in Phyllodocida and Myzostomida, ventral pharyngeal organs are widely distributed among different polychaete taxa, including Aciculata, Canalipalpata, and Scolecida (Dales 1962; Purschke 1988a; Purschke and Tzetlin 1996). A VPHO armoured by specific jaws consisting of ventral paired mandibles and lateral maxillae is a character considered to be apomorphic to Eunicida (Kielan-Jaworowska 1966; Tzetlin 1980; Wolf 1980; Purschke 1987). That is why data on the occurrence of jaws in the representatives of another polychaete group, Terebellida (Canalipalpata), is important for our understanding of the evolution of the mouth parts in Polychaeta.

Three taxa within Terebellida are presently known to have a VPHO armoured with jaws, all of them smaller species of Ampharetidae. Desbruyères (1978) described *Gnathampharete paradoxa* and the next report was made by Uebelacker

(1984), who described a few specimens of *Ampharete* sp. B with a transversal row of tooth-like structures. Mackie (1994) described a new genus and species *Adercodon pleijeli* with a ventral pharyngeal organ armoured by a transversal row of 30–40 triangular teeth.

Desbruyères (1978) considered the occurrence of jaws in *G. paradoxa* as a unique, aberrant case and, at the same time, as important evidence of the homology of the ventral pharyngeal organs in Terebellida and Eunicida. However, he did not specify whether the jaws of *Gnathampharete* should be considered homologous to the mandibles or maxillae of Eunicida. Desbruyères (1978) and later Holthe (1986) stated that the presence of jaws in Ampharetidae is a manifestation of an ancestral state, but most likely not functional. These authors believed jaw-bearing polychaetes to be predators and were surprised to find predators among the Ampharetidae.

Mackie (1994) suggested that the transversal row of teeth located on the posteriormost edge of the VPHO could be used for the sorting of food particles in *Aderocodon*, though he agreed with the two previous authors that the jaw-like structures in some Ampharetidae seemed to be an ancestral character state. Contrary to Desbruyères other authors (Purschke 1988a; Purschke and Tzetlin (1996), Tzetlin and Purschke (2004) and Zhadan and Tzetlin (2002)) have proposed that the VPHO found in some members of the Canalipalpata, Scolecida and the so-called archiannelid groups of polychaetes (Flabelligeridae, Ctenodrilidae, Spionidae, Terebellida, Arenicolidae, Maldanidae, Orbiniidae, Diurodrilidae, Nerillidae Protodrilidae and Saccocirridae) most likely evolved independently from the eunicid VPHO.

Terebellida (s. stricto) includes Ampharetidae, Terebellidae, Trichobranchidae, Pectinariidae, and Alvinellidae (Holthe 1986; Rouse and Pleijel 2001). These taxa are characterized by a well-developed ventral pharyngeal organ. These organs are found in both adults and juveniles. In adults, the VPHO seems to be used for treatment of food particles in the pharyngeal cavity, whereas in early juveniles it is the main feeding structure. Juveniles have only one to three short rudimental buccal tentacles useless even for collecting food particles (Heimler 1983). They feed by applying the VPHO directly to the substrate. At this stage of ontogeny, the VPHO is represented by a ventral bulb consisting of muscle cells and interstitial cells. The general appearance of this structure is very similar to that of the VPHO of Dinophilidae; furthermore, it also has the same function, being used for scraping off microfouling from the substrate (Tzetlin 1987; Tzetlin *et al*. 1987). In the adult stages, the function of feeding is passed to the numerous buccal tentacles, while the VPHO takes part in the sorting of sediment particles and the formation of food conglomerates (Dales 1955; Sutton 1957). These data were obtained for members of Terebellidae, but were presumed to be true also for the closely related families: Ampharetidae, Trichobranchidae, Alvinellidae, and Pectinariidae (Zhadan and Tzetlin 2002). All three jaw-bearing species of Ampharetidae are very small worms as adults, being only a few millimeters long. From a functional point of view they could be directly compared with the early juveniles of the larger species of Ampharetidae; their VPHOs are most likely to function as organs used for scraping of microfouling.

Previous descriptions of the jaw structures in Ampharetidae so far are based on light microscopical observations (Desbruyères 1978; Uebelacker 1984; Mackie 1994). The microanatomy of the ventral muscle bulb, the exact location of the teeth, the ultrastructure of their cuticle and hard parts, and the mode of jaw growth are largely unknown. The present paper seeks to rectify this situation.

Material and methods

Material examined

Adercodon pleijeli Mackie (1994):
Paratypes 1 and 2: sample 8, Banyuls-sur-Mer, France 42°29,75′ N, 3°09,00′ E, sandy mud, 32 m, 11 Oct 1991, N.M.W.Z. 1992.003.8 and NMW.Z. 1992.003.9.

Paratype 3: sample T-15, off Azi-Castello, Sicily, Italy 37°32,50′ N, 15°10,80′ E, muddy sand, 90–95 m, 17 May 1990, N.M.W.Z. 1992, 002.2.

4 specimens: sample 11, off Banyuls-sur-Mer, France, 42°29,75′ N 3°09,00′ E, muddy sand, 30 m, 15 May 1997. NMW.Z. 1997. 031.

Ampharete sp. B *sensu* Uebelacker (1984):
2 specimens. Station V-2529, off Panama City, Florida, Gulf of Mexico, 29°55 59′ N, 86°06 29′W, sandy silt, 38 m, 1 Jun, 1975 USNM 71424.

Methods

Two jaw-bearing specimens of *Ampharete* sp. B *sensu* Uebelacker (1984) USNM 71424, were fixed in a formalin solution and stored in 70% alcohol. The specimens were studied with the help of a Scanning Electron Microscope (SEM) after sagittal dissection. For SEM observation specimens were dried at critical point after dehydration in an ethanol series and acetone, and later coated with gold prior to their examination with a Hitachi 400 A scanning electron microscope.

Three paratypes of *Adercodon plejeli* collected in 1991 were fixed in buffered formalin and stored in 70% alcohol. Specimens of *Adercodon pleijeli* collected in 1997 were fixed in 2.5% glutaraldehyde, buffered with 0.2 M sodium cacodylate buffer (pH = 7.2–7.4) with 0.36 M sucrose added and post-fixed, after rinsing, with 1% osmium tetroxide in the same buffer. For transmission electron microscopy (TEM), fixed specimens were dehydrated in an ethanol series and acetone before being embedded in Epon. Semi-thin (1.0 = 0.5 μm) and ultra-thin (50–80 nm) sections were cut on a Dupont Sorwall Ultramicrotome. Semi-thin sections were stained in a 1% solution of toluidine blue in water. Ultrathin sections for TEM observation were stained in lead citrate and uranyl

acetate and then examined with a JEOL 1200 transmission electron microscope. Two series of semithin sections (transversal and sagittal) and two complete series of ultrathin sections (transversal and sagittal) through the anterior part of the body were prepared from four specimens collected in 1997.

Results

Examined specimens are referred to through their generic names (*Adercodon* and *Ampharete*). Despite their belonging to two different genera, the general anatomy of the mouthparts is very similar in the two species studied. The mouth opening lies directly behind the prostomium and leads to the buccal cavity. The upper lip bears mouth tentacles located on the inner surface of the buccal cavity immediately behind the mouth (Figs 1 and 3). The ventral pharyngeal organ is situated on the ventral surface of the cavity (Figs 1 and 3). The epithelium of the buccal cavity is covered by a thin cuticle. The epithelial cells bear no cilia and no glandular cells were found in this region of the digestive tract. The anterior opening of the oesophagus is located in the hind part of the buccal cavity (Figs 1 and 3A). When the mouth tentacles and the upper lip protrude from the mouth, the anterior part of the oesophagus resembles an epithelial tube with a relatively narrow lumen, shifted into the buccal cavity (Figs 1 and 4A). When the upper lip is contracted, the mouth tentacles occupy the anterior part of the oesophagus (Fig. 3A). The specimens for both species studied have 14 to 18 mouth tentacles of about 30 μm in diameter each.

In both species, the VPHO is situated on the ventral side of the buccal cavity. It is composed of a ventral bulb and investing muscle fibres (Figs 1, 3A,B and 4A,C). The bulb consists of posterior and anterior parts separated by a deep median transversal groove. In *Adercodon pleijeli* the VPHO is 160 μm wide. Along the longitudinal axis of the body, the anterior part of the ventral bulb (between ventral invagination and median groove) measures about 180 μm and the posterior part (behind median groove) is about 100 μm long. In *Ampharete* sp. B the length of the ventral part of the VPHO

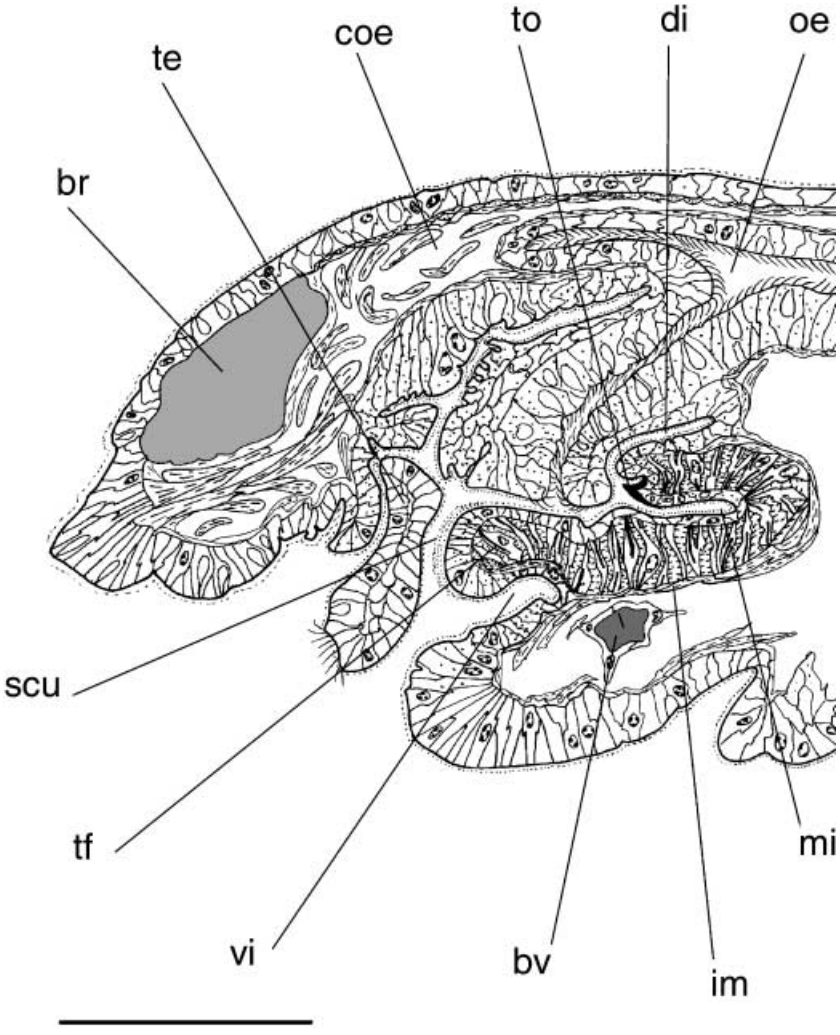


Fig. 1—*Adercodon pleijeli*. Sagittal section through anterior part of the body. Mouth tentacles half protracted from the mouth. Ventral muscle bulb retracted deep inside buccal cavity. Scale – 100 μm. br – brain, bv – blood vessel, coe – coelom, di – dorsal invagination, im – investing muscle cell, mi – medial invagination, oe – oesophagus, scu – specialized cuticle, te – mouth tentacle, tf – tonofilament, to – tooth, vi – ventral invagination.

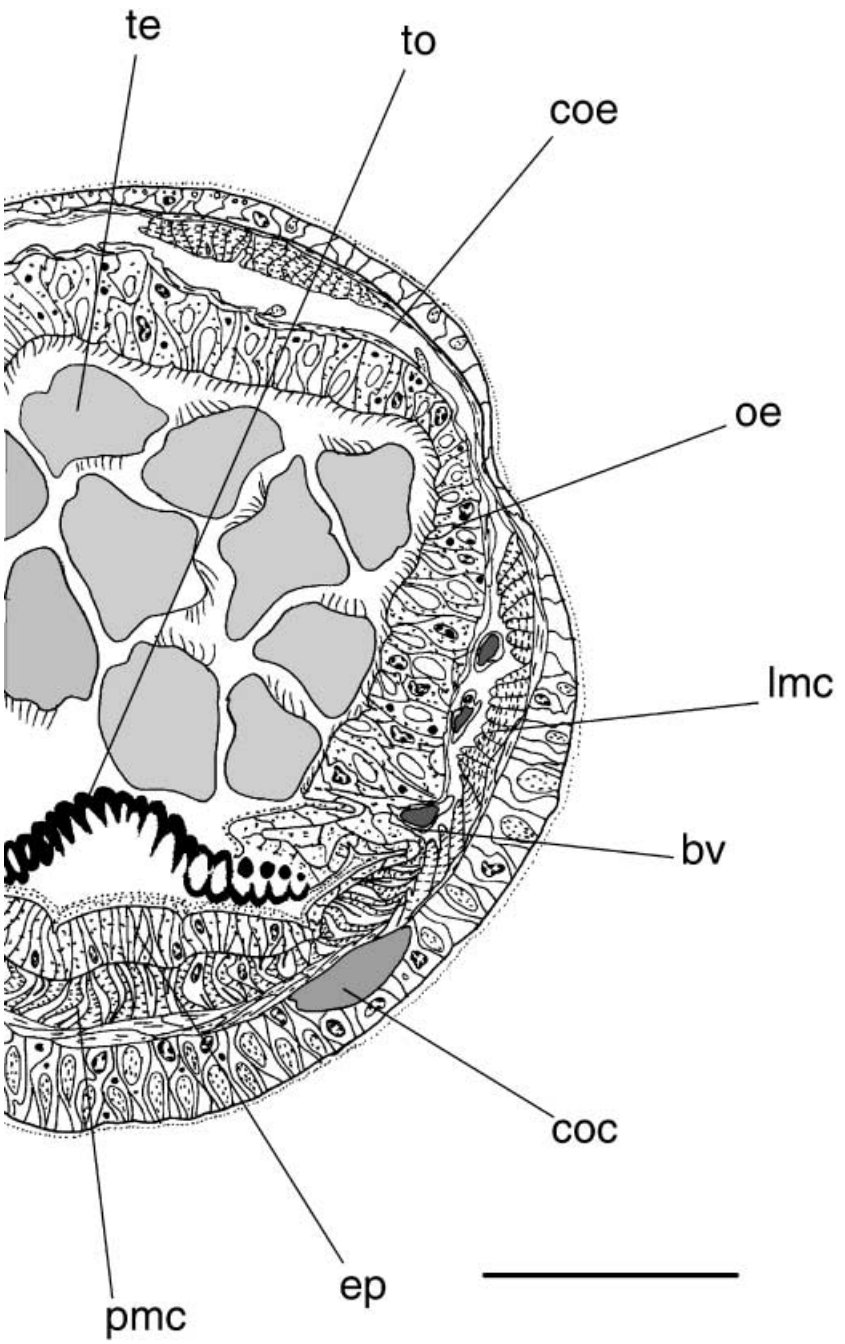
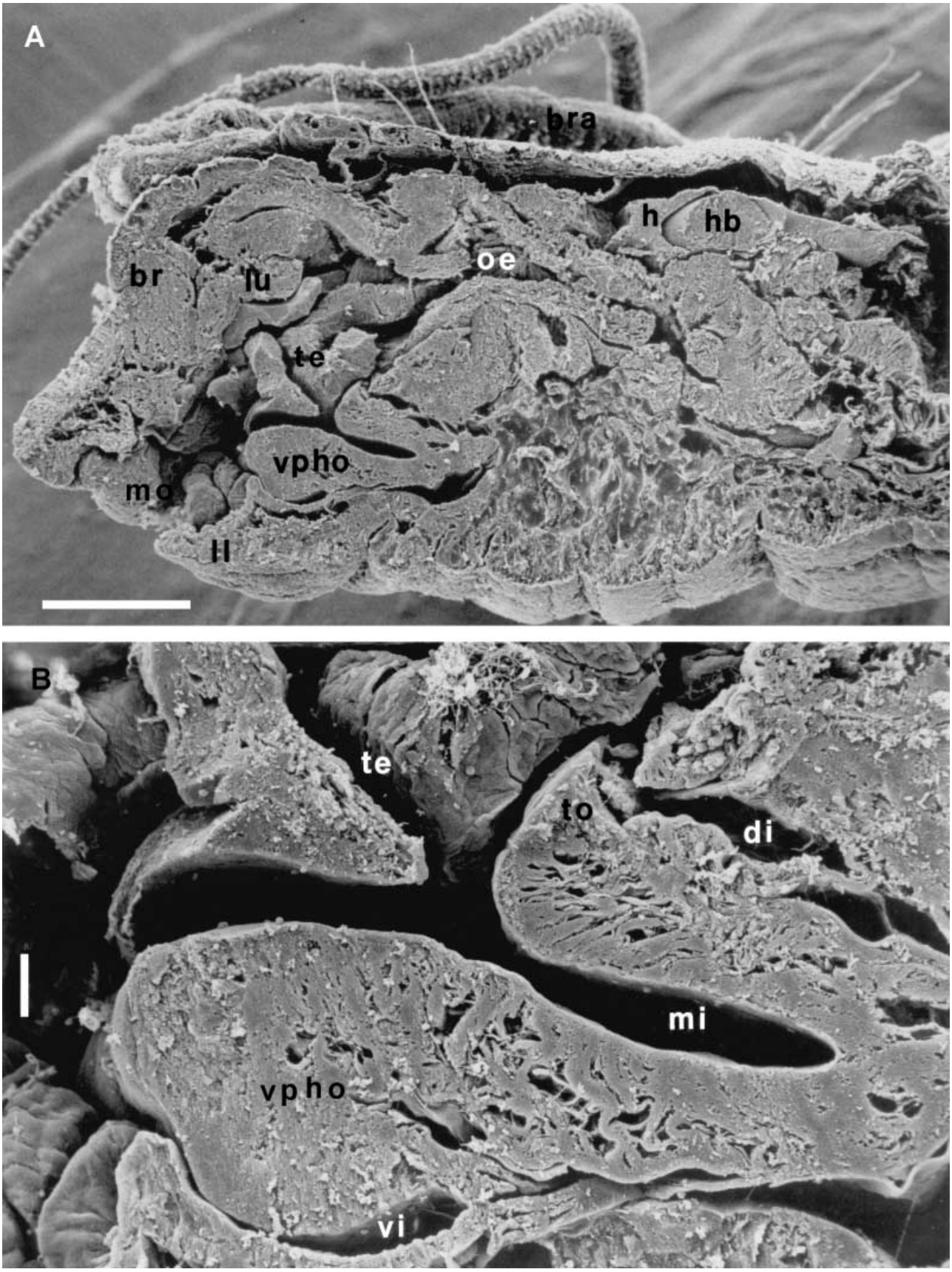


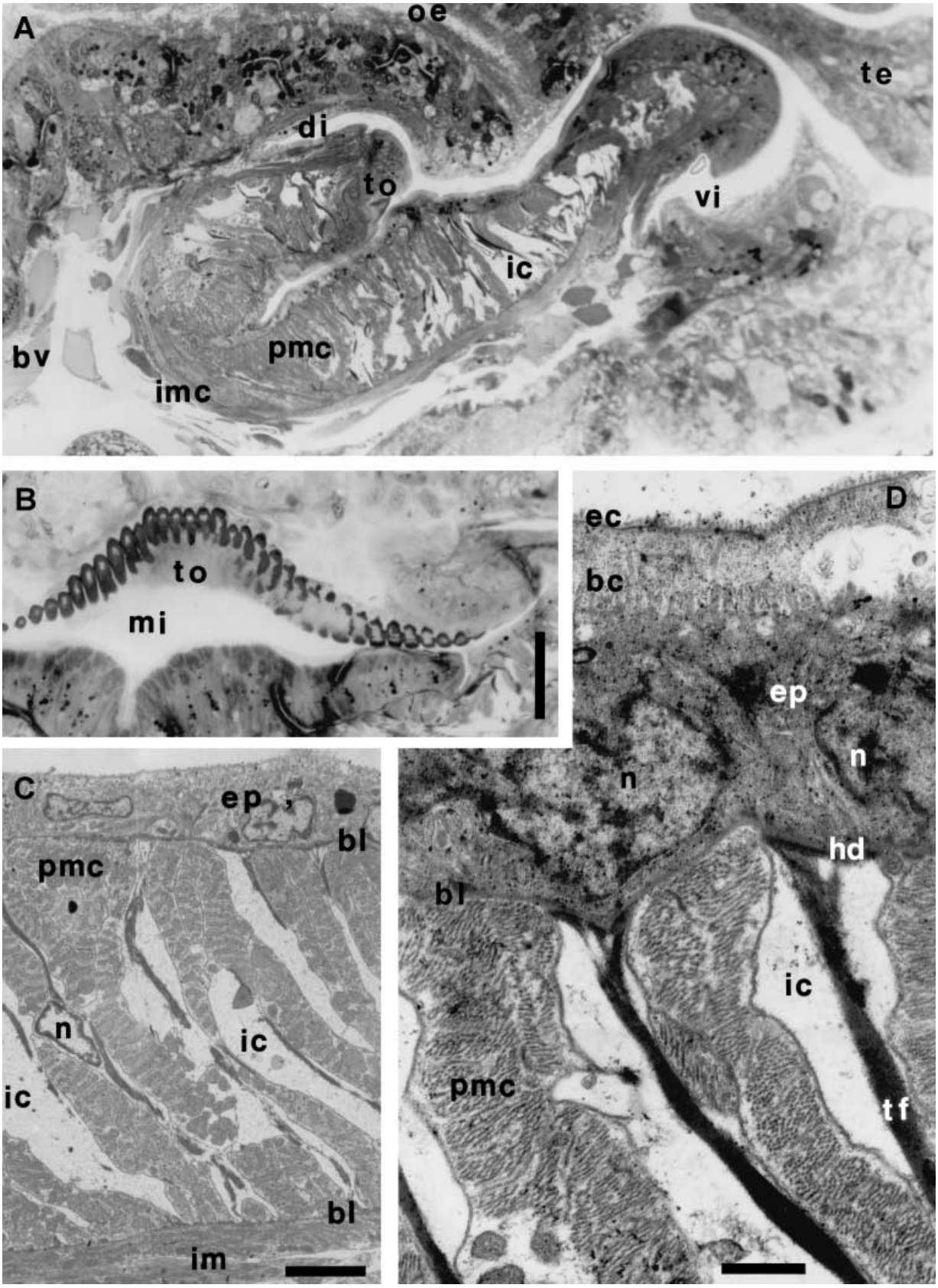
Fig. 2—*Adercodon pleijeli*. Transversal section through anterior part of the body, behind mouth opening, at the level of the transversal row of denticles (teeth). Mouth tentacles retracted into the buccal cavity. Scale – 100 μm. bv – blood vessel, coc – circumoesophageal connective, coe – coelom, ep – epithelium, lmc – longitudinal muscle cell, oe – oesophagus, pmc – plate muscle cell, te – mouth tentacle, to – tooth.

(between the ventral invagination and the median groove) is 195–200 μm and the posterior part is about 135 μm long.

The anterior part of the bulb has a three-lobed structure. In both species, the triangular teeth or denticles are arranged in a single transversal row on the surface of the posterior part of the ventral bulb just in front of its posterior edge (Figs 1, 2, 4B and 5A). As in the resting pharynx the whole ventral bulb is V-shaped in the sagittal plane, and the teeth are

Fig. 3—*Ampharete* sp. B from the Gulf of Mexico. —**A**. Sagittal section through anterior part of the body (right part); —**B**. Fragment of the same section, ventral pharyngeal organ (SEM). Scale: A – 100 μm, B – 10 μm. br – brain, di – dorsal invagination, h – heart, hb – heart body, ll – lower lip, lu – upper lip, mo – mouth, mi – medial invagination, oe – oesophagus, te – mouth tentacle, to –tooth, vi – ventral invagination, vpho – ventral pharyngeal organ.





orientated frontally within the buccal cavity (Fig. 1). The number of denticles varies from 36 to 40 in *Adercodon pleijeli* and is about 50 in *Ampharete* sp. B. The height of the denticles is about 6–7 μm in *A. pleijeli* and 10–12 μm in *Ampharete* sp. B.

The ventral bulb of *A. pleijeli* is covered by a one-layered epithelium. The thickness of the epithelium averages 2.0 μm and the nuclei are elongated and about 2.1 μm long (Fig. 4C,D). The cuticle of the bulb is of two different types: the regular cuticle covering most of the bulb and a specialized intermediate cuticle surrounding the base of the teeth and the frontal surface of the anterior part of the ventral bulb (Figs 4D, 5C,F).

The thickness of the regular cuticle is about 0.865 μm. The epicuticle consists of an electron-dense layer that is 0.06 μm thick. The basal cuticle is penetrated by microvilli. Amorphous collagen fibres lie in the basal cuticle among the microvilli.

Ultrastructure of jaws

Each tooth is composed of two main layers. The dental (outer) one is the electron-dense sclerotized layer that covers the tooth. The inner one consists of long microvilli within a collagen matrix (Fig. 5B,C). The thickness of the dental layer ranges from 0.95 to 0.6 μm. The microvilli situated in the inner layer of the tooth are about 4 μm long. The thickness (diameter) of the microvilli is about 0.1 μm, which is about twice as large as that in the microvilli forming the basal cuticle of the regular cuticle on the bulb surface.

The electron-dense material which forms the outer sclerotized dental layer of the teeth was also found in the outer part of the basal cuticle, as separate electron-dense granules, 30–60 nm in cross section, situated between the microvilli. The concentration of these granules gradually increased from the basal to the distal zone of the teeth (Fig. 5B,C,D,E).

The gnathoblasts do not differ significantly from neighbouring epithelial cells. They are about 7 μm high and their nuclei are about 3.5 μm in diameter. The only difference between them is the presence of a layer of electron-transparent vesicles about 0.25 μm in diameter in the distal part of the gnathoblasts (Fig. 5C).

Each tooth is surrounded by a band of specialized cuticle. This cuticle can be considered as an intermediate zone between the regular cuticle covering the bulb and the solid jaw. In this zone the thickness of the cuticle ranges from 1.3 to 2.75 μm, epicuticle is absent, and the basal cuticle is formed by long and very densely arranged microvilli. This intermediate type of cuticle is formed by two concentric circles of epithelial cells. The inner row, closest to the denticle, forms the outer edge of the tooth and its cells can be considered as gnathoblasts, but the outer one does not form the electron-dense material seen in the teeth. Epithelial cells which form this type of cuticle contain electron-transparent vesicles that have a diameter of 0.2–0.7 μm, similar to those of the gnathoblasts.

A similar type of cuticle covers the anterior frontal surface of the bulb, immediately behind the ventral invagination (Fig. 5F). No evidence of tooth replacement was found in either of the species studied.

The muscle system of the ventral bulb is quite similar in the two species. Both posterior and anterior parts consist of regularly arranged plate-shaped cells with transversally orientated myofilaments and interstitial cells. The latter are armoured with bundles of tonofilaments. Both parts of the ventral bulb are underlain with investing muscle fibres. In this species, the plate-like muscle cells are 14–15 μm high. They extend from the bulb epithelium to the investing muscle layer.

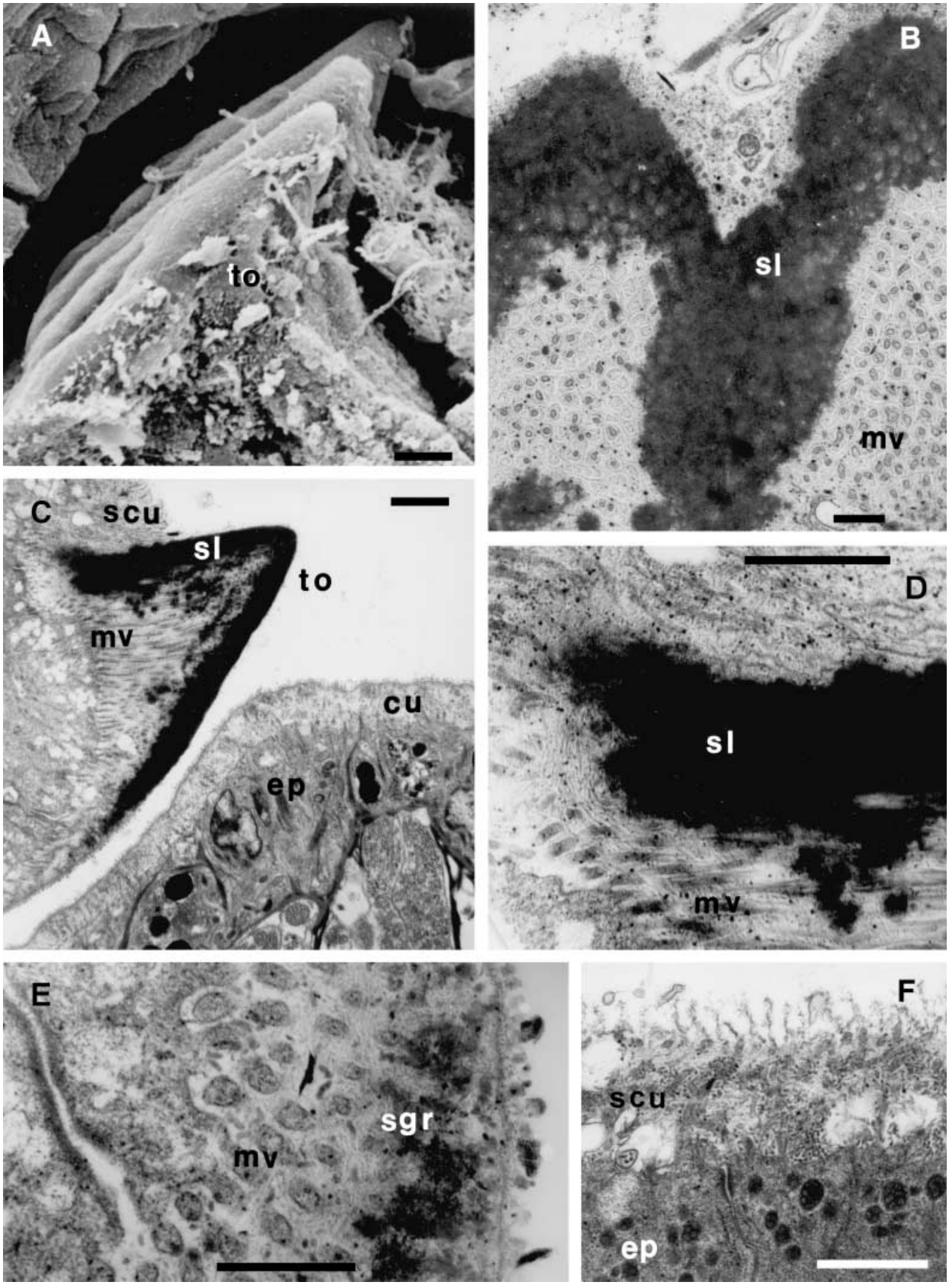
The plate-like muscle cells of the bulb are obliquely striated and of the circomyarian type. The elongated nuclei, 2–3 μm long, and mitochondria, 0.3–0.8 μm in diameter, are situated in the middle part of the cell and, consequently, in the middle zone of the VPHO. The bundles of myofilaments are arranged along the cell membrane and always run parallel to the fibre axis, i.e. transversally. Bundles of myofilaments consist of thick and thin myofilaments arranged in the manner that is typical of obliquely striated fibres.

The interstitial cells are arranged regularly between the plate muscle cells in such a way that an interstitial cell, extending from the bulb epithelium to the basal muscle capsule (investing muscle), is located between every two plate muscle cells. Bundles of tonofilaments run from the bulb basement to the epithelium and reach up to 0.5 μm in diameter (Fig. 4D). In the zone close to the extracellular matrix, the bundles of tonofilaments are branched into several parts, each anchored in the extracellular matrix of the bulb epithelium by hemidesmosomes. The muscle capsule of the VPHO, i.e. investing muscle, is about 5.3 μm thick. It consists of a layer of longitudinal muscle cells (Figs 1 and 4A,C).

Discussion

The ventral pharyngeal organs of the two species studied are very similar in structure: the ventral muscle bulb contains plate muscle cells and regularly arranged interstitial cells. As *Ampharete* sp. B was studied only with SEM, it was not

Fig. 4—*Adercodon pleijeli*. —**A**. Ventral pharyngeal organ, sagittal semithin section; —**B**. Denticles and ventral pharyngeal organ, transversal semithin section; —**C**. Fragment of transversal section through VPHO, TEM; —**D**. Fragment of sagittal section through VPHO, TEM. Scale: A – 20 μm, B – 20 μm, C – 2 μm, D – 1 μm. Bc – basicuticle, bl – Basal lamina, bv – blood vessel, di – dorsal invagination, ec – epicuticle, bc – basicuticle, ep – epidermal epithelium, hd – hemidesmosome, ic – interstitial cell, imc – investing muscle cell, mi – medial invagination, n – nucleus, oe – oesophagus, pmc – plate muscle cell, te – mouth tentacle, tf – tonofilament, to – tooth, vi – ventral invagination.



possible to observe whether its interstitial cells have transversal dorsoventral tonofilaments, as in *Adercodon*. However, the presence of transversal tonofilaments in the interstitial cells of the ventral bulb has been verified in young specimens of *Ampharete arctica* (Tzetlin 1992). These tonofilaments are characteristic of the ventral bulb of Ampharetidae, although have also been found in other Terebellida as well (Zhadan and Tzetlin 2002). A ventral bulb with interstitial cells has been found in many polychaete taxa (Purschke 1988b), such as Ctenodrilidae and Orbiniidae that comprise Canalipalpata and Scolecida. Following the phylogeny presented by Rouse and Fauchald (1997) this means that such a muscle bulb represents a character complex that evolved early in the stem lineage of polychaetes and has been lost and replaced by different pharyngeal structures in Aciculata. Alternatively, these two taxa, Scolecida and Canalipalpata, may in fact be sister groups. This problem is in part related to the question of how to root the annelid tree and has been discussed repeatedly (e.g.; McHugh 1997; Westheide 1997; Rouse and Pleijel 2001; Purschke 2002).

In both species studied the ventral bulbs are similar in size and position. Moreover the structure of the denticles is identical. In both cases a transversal row of denticles is situated on the posterior edge of the ventral bulb. The denticles are also similar in size (6–12 μm in height).

What could be the function of the denticles of *Adercodon pleijeli* and *Ampharete* sp. B? It seems that they could play a certain role in scraping off microfouling. According to Tzetlin *et al.* (1987), early juveniles of terebellids use their ventral bulb for scraping off microfouling while their tentacular apparatus is still poorly developed and not functional. Both species referred to in the present paper are very small animals; their body sizes are comparable with that of juveniles of other terebellidans. They can use both their mouth tentacles and VPHO for feeding, the latter similar to numerous tiny Dorvilleidae, Nerillidae, and Protodrilida which either have scraping jaws or a thick cuticle on the surface of the ventral muscle bulbs (Purschke and Tzetlin 1996).

The teeth of *Adercodon* are formed by gnathoblasts, which are specialized epithelial cells. These cells form a layer of long microvilli. The teeth are characterized by an electron-dense outer dental layer and a thick basal layer penetrated by microvilli. The dental layer is formed by the deposition of a secretion between the microvilli. Therefore, the fine structure of the jaws in Ampharetidae is very similar to that of the mandibles of Dorvilleidae, the mandibles and maxillae of Lumbrineridae, Eunicidae and Onuphidae (Eunicida), and the jaws of Glyceridae, Polynoidae, and Nereididae (Phyllodocida) (Wolf 1980; Purschke 1988a). Jaws of this type are characterized by unlimited growth and the absence of any replacement in all studied cases (Wolf 1980; Paxton 1980). No evidence of replacement (shedding) of the denticles, like that observed in the maxillae of Dorvilleidae (Purschke 1987, 1988a) was found in the present study.

The position of the sclerotized structures in the buccal cavity of Ampharetidae is similar to the location of the transversal band of papillae found in the pharyngeal cavity of *Alvinella pompejana* (Alvinellidae) (Desbruyères and Laubier 1991). Saulnier-Michel *et al.* (1990) described the papillae as structures having a thick cuticle. The presence of sclerotized structures on the posterior part of the ventral muscle bulb could represent a common character for both families.

The ultrastructure of the teeth and gnathoblasts in the two species studied here are very similar to that of the same structures in other jaw-bearing polychaetes. In all cases the jaws are formed from a special type of sclerotized cuticle. However, the evidence that the maxillae and mandibles of Eunicida are homologous to the jaws of Ampharetidae is poor. In Eunicida only one component of the pharyngeal armature, the mandibles, is situated in the area of the ventral bulb (maxillae are formed by lateral folds, the lateral muscular structures of VPHO). In the initial stage of their development, eunicidan mandibles are represented solely by a transversal row of poorly sclerotized denticles divided into right and left groups. Later these two groups of denticles form the frontal denticulated surface of the right and left mandibles, respectively (Tzetlin 1980). The transversal row of denticles in the Ampharetids studied here is located on the posterior part of the bulb; it is a single row with no evidence of paired structures. Mandibles of Eunicida cover a significant part of the bulb surface, mostly its anterior part (Purschke 1987). For this reason the jaw-like structures situated on the ventral bulb of some Ampharetidae and Eunicida should be considered the result of homoplastic derivation. Consequently, the occurrence of jaws in a few smaller Ampharetidae is an apomorphic state. Further studies of more inclusive material are required to determine whether Ampharetidae with an armoured ventral pharyngeal organ form one taxon or not.

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Fig. 5—*Ampharete* sp. B from the Gulf of Mexico. —**A**. Transversal row of denticles (teeth), SEM; *Adercodon pleijeli*, —**B**. Fragment of a transversal section through the row of teeth, TEM; —**C**. Sagittal section through the teeth, TEM; —**D**. Fragment of the basal part of the tooth, microvilli of the gnathoblast and sclerotized granulae, sagittal section, TEM; —**E**. Electron-dense granulae – centres of sclerotization in the basicuticle of the gnathoblast, sagittal section, TEM; —**F**. Specialized type of cuticle in the frontal zone of the lower part of the ventral bulb (note long microvilli and the absence of an epicuticular layer), sagittal section, TEM. Scale: A – 2 μm, B – 0.5 μm, C – 1.5 μm, D – 1.0 μm, E – 0.5 μm, F – 1.0 μm cu – cuticle, ep – epidermal epithelium, mv – microvilli, scu – specialized cuticle, sgr – sclerotized granulae, sl – sclerotized dental layer, to – tooth.

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