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Formation of marginal radular teeth in Conoidea (Neogastropoda) and the evolution of the hypodermic envenomation mechanism

Yuri I. Kantor[1] and John D. Taylor[2]

[1] A. N. Severtzov Institute of Problems of Evolution, Russian Academy of Sciences, Leninski prosp. 33, Moscow 117071, Russia. E-mail: kantor@malaco-sevin.msk.ru
[2] Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. E-mail: j.taylor@nhm.ac.uk

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Abstract

Four main types of radula are found within the gastropod superfamily Conoidea. Type 1, the Clavidae type has five teeth in each row with comb-like laterals and flat pointed marginals. Type 2, the Turridae type has two or three teeth in a row with the marginals comprised of teeth with the duplex or wishbone form. Type 3, the Pseudomelatomidae/Pervicaciinae type has two or three teeth in a row with the marginals curved and solid. Type 4, the hypodermic type has two hollow, enrolled, marginal teeth in each row with the radular membrane reduced or absent. Study of the maturing teeth along the radular membrane in gastropods with the Type 2 radula shows that the duplex teeth are not formed from two separate elements but develop from a flat plate, by thickening of the tooth edges and elevation of the posterior edge from the membrane. Semi-enrolled and enrolled teeth of *Pilsbryspira*, *Imaclava* and *Toxiclionella* develop in a similar way. In Conidae where a vestigial radular membrane is attached only at the base of the teeth, the teeth are enrolled from first formation in the radular sac. This study demonstrates that duplex and enrolled teeth develop by a similar process, allowing the possibility of deriving hypodermic teeth from duplex clades as has been suggested by previous phylogenetic analysis.

Key words: gastropods, Conoidea, radular teeth, development

INTRODUCTION

Gastropods of the superfamily Conoidea (= Toxoglossa) are notable for the possession of a large venom gland, together with highly modified radular teeth which are held at the proboscis tip and used to inject venom into their prey. The feeding process has been most studied in species of *Conus* which possess elongate, barbed, harpoon-like teeth (Kohn, 1990; Olivera *et al*., 1990; Kohn, Nishi & Pernet, 1999), but conoideans with other types of teeth also envenomate their prey. Over the last 10 years or so anatomical investigations of conoidean gastropods have revealed a great disparity of foregut anatomies, and characters defined in these studies have been used to help unravel phylogenetic relationships (Sysoev & Kantor, 1989; Taylor, 1990; Taylor, Kantor & Sysoev, 1993; Kantor, Medinskaya & Taylor, 1997). However, the evolutionary pathways whereby hollow, harpoon-like teeth might be derived from 'normal' gastropod teeth are still unclear, as are the homologies between the different types of teeth found within the Conoidea.

Radular morphology is very variable within the conoideans but four main types can be recognized (Fig. 1):

Type 1: the Clavidae type is characterized by having five teeth in each transverse row, comprising a small central tooth, two large, comb-like, lateral teeth and two, usually flat-bladed, marginal teeth. This radular type is found only in the family Clavidae (Fig. 1a).

Type 2: the Pseudomelatomidae/Pervicaciinae type has two or three teeth in a row, comprising solid, curved and pointed marginals and often a plate-like central tooth (Fig. 1c). The marginal teeth are attached to the membrane by rather a narrow base and therefore free along most of their lengths. This dentition characterizes the families Pseudomelatomidae, Strictispiridae and Pervicaciinae (Terebridae), but there is no central tooth in pervicaciines and strictispirids. In the Pervicaciinae and Strictispiridae (Kantor & Taylor, 1994) the venom gland is absent, and the Pseudomelatomidae do not use marginal teeth for stabbing prey (Kantor, 1988).

Type 3: the Turridae type of radula has two or three teeth in each row, comprising a central tooth (often

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*All correspondence to: J. D. Taylor

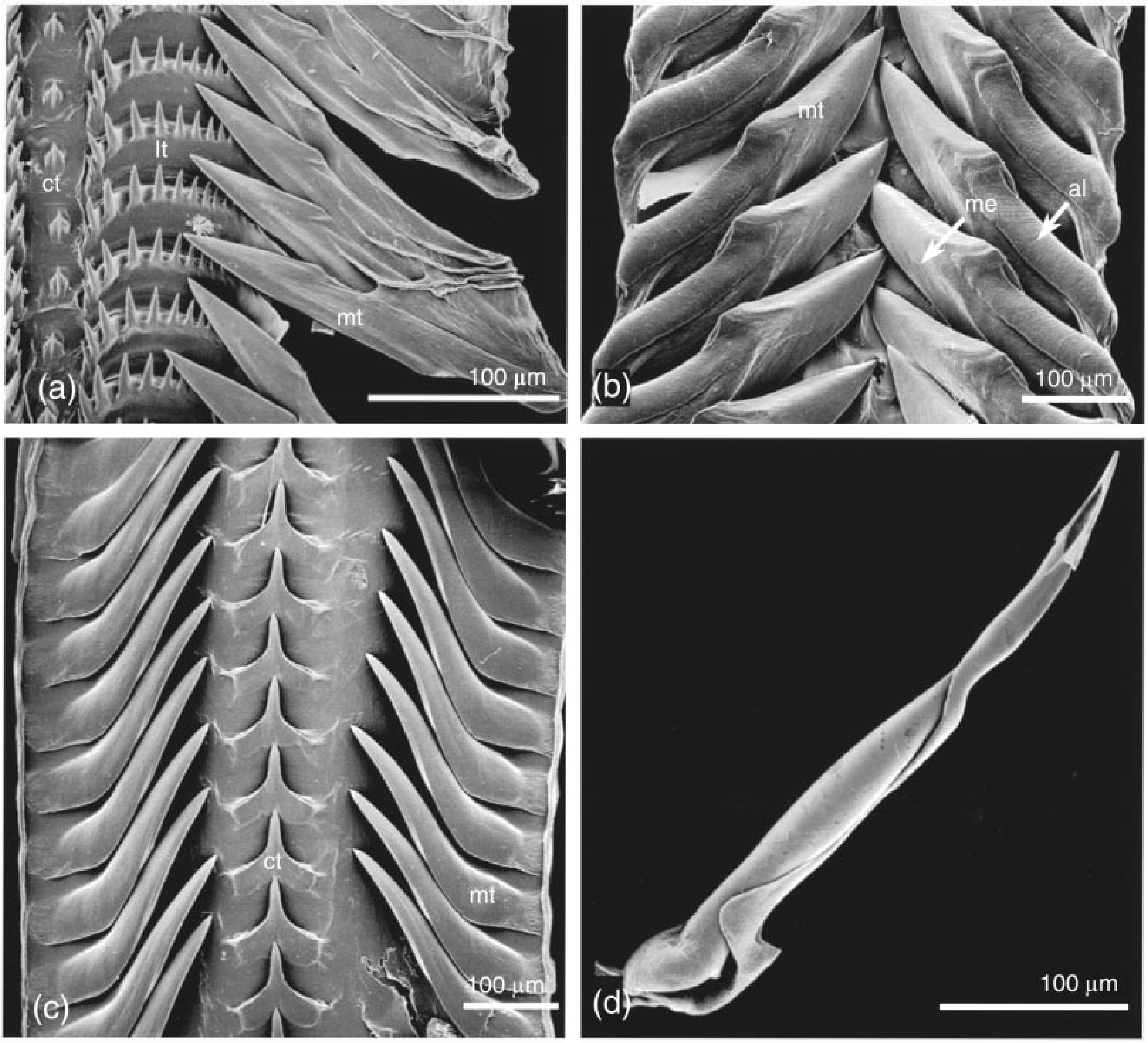

Fig. 1. Four main types of radula within Conoidea. (a) The clavid type, *Clavus* sp. (Clavidae). (b) The turrid type, *Clionella sinuata* (Born, 1778) (Turridae). (c) The pseudomelatomid type, *Pseudomelatoma penicillata* (Carpenter, 1864). (Pseudomelatomidae). (d) The hypodermic type, *Conus boholensis* Petuch, 1979 (Conidae). Abbreviations: al, accessory limb; ct, central tooth; lt, lateral tooth; me, major element; mt, marginal tooth.

absent) flanked by a pair of marginals. In most cases the marginals are of the so-called wishbone (or duplex; Maes, 1971) morphology (Fig. 1b). Usually, the duplex tooth consists of a robust, pointed, major element and a smaller, more slender, accessory limb (Fig 1b). Illustrations of duplex teeth using light microscopy show different arrangements of the elements. The base of the accessory limb may appear to be: attached to the radular membrane; attached to the major element; or even free at the base with the tooth having the shape of a clothes peg. The major elements of the marginal teeth are attached to the membrane along most of their length and only the tips are free. A wide variety of different duplex tooth morphologies has been illustrated (e.g. Powell, 1966, figs B–D; McLean, 1971, figs 27–79). This type is the most variable in morphology and is characteristic of the family Turridae.

Type 4: the hypodermic type is characterized by the presence of two hollow, enrolled, marginal teeth in each row, with the subradular membrane much reduced or absent (Fig. 1d). This type of radula is found both in the family Conidae (sensu Taylor *et al.*, 1993) and also in some Terebridae, in which it has been independently derived. It has been generally accepted that in conoideans with this type of radula the radular membrane is either absent (Kohn, Nybakken & Van Mol, 1972; Shimek, 1975; Taylor *et al.*, 1993) or vestigial (Shimek & Kohn, 1981). In *Conus* (Marsh, 1977) and *Oenopota* *levidensis* (Shimek, 1975), it has been shown that each tooth is apparently attached to the pavement epithelium of the radular sac by its own separate ligament which is similar histochemically to initially forming teeth. The ligament is an elongate, flexible stalk, attached to the base of the tooth. In *Conus* it is subcircular in cross-section and long in some species. Ligaments are often visible on scanning electron micrographs of Conus teeth, although they are usually flat and membrane-like (Fig. 6a). The ligaments have been considered to be homologous with the radular membrane of other gastropods (Marsh, 1977).

Marginal teeth which are similar and even sometimes indistinguishable from the hypodermic teeth of Type 4 are found in some species of groups normally possessing the Type 1 radula (family Clavidae, genus *Imaclava*) (Fig. 4a–c) and Type 3 radula (Turridae, genera *Pilsbryspira, Toxiclionella* and *Ptychobela*) (Fig. 4d–f, 5d). Nevertheless, these mentioned genera have anatomical characters similar to other members of the corresponding groups. Moreover, the radular membrane in these species is distinct and the teeth are attached to it along most of their lengths.

Phylogenetic analysis (Taylor *et al.* 1993; Kantor *et al.* 1997) demonstrated that both typical hollow, harpoon like hypodermic teeth as well as various other types of enrolled teeth evolved repeatedly and independently in different conoidean clades. This analysis also suggested that the Conidae were derived from a clade possessing Type 3 wishbone teeth.

The phylogenetic analysis also suggests that the Type 1 teeth of the Clavidae with blade-like marginal teeth are the least derived for the Conoidea (Taylor *et al.*, 1993). The evolutionary origin of duplex teeth has been the subject of some speculation. Maes (1971) suggested that the smaller element ('accessory limb') might be the evolutionary remnant of a missing extra pair of marginal teeth. By contrast, Shimek & Kohn (1981) illustrated in two species, *Knefastia dalli* (Cochlespirinae) and *Crassispira rudis* (Crassispirinae), the probable derivation of the accessory limb from a fold in the developing marginal tooth.

Our preliminary observations of the sequentially maturing duplex teeth on the early forming parts of the radular ribbon of *Comitas* species (Cochlespirinae) showed that the duplex teeth appeared to develop from flat, plate-like structures. These observations suggested that a study of the development of different types of duplex teeth may help understand their formation and determine their homologies with other types of conoidean teeth. We thus studied maturing teeth in a variety of conoideans possessing duplex teeth and also examined the developing teeth of Clavidae (Type 1), as well as different types of enrolled hypodermic teeth in *Imaclava* and *Toxiclionella*. One of the main questions we had in mind was whether gastropods with hypodermic teeth could have evolved from clades with duplex teeth as was suggested by the phylogenetic analysis.

MATERIALS AND METHODS

Radulae were dissected from the gastropods and then cleaned in dilute sodium hypochlorite solution taking care to preserve the fragile distal portions. They were then washed in distilled water, mounted without adhesive onto circular glass cover slips and air-dried. The cover slips were then glued to aluminium stubs, sputter-coated with Au/Pd alloy and examined by scanning electron microscopy (SEM). Serial sections of foreguts were cut at 8 μm and stained in green Masson's trichrome.

List of species examined with collection localities

Pseudomelatomidae: *Pseudomelatoma penicillata* (Carpenter, 1864) Mexico; **Clavidae**: *Imaclava pilsbryi* (Bartsch, 1950) Panama; *Clavus* sp. Guam; **Turridae: Turrinae**: *Xenuroturris cingulifera* (Lamarck, 1822) Hansa Bay, New Guinea, *Lophiotoma acuta* (Perry, 1811) Hansa Bay, New Guinea; **Cochlespirinae**: *Cochlespira pulchella* (Schepman, 1913) Indonesia; *Comitas murrawolga* (Garrard, 1961) New Caledonia; *Comitas onokeana vivens* Dell, 1956 SW Pacific, off Fiji; **Clavatulinae**: *Clionella sinuata* (Born, 1778) South Africa; *Toxiclionella tumida* (Sowerby, 1870) South Africa; **Crassispirinae**: *Funa jeffreysii* (Smith, 1875) Hong Kong; *Cheungbeia robusta* (Hinds, 1843) Hong Kong; *Ptychobela suturalis* (Gray, 1838) Hong Kong; **Zonulispirinae**: *Pilsbryspira nympha* (Pilsbry & Lowe, 1932) Mexico; **Conidae**: *Conus anemone* Lamarck, 1810 Rottnest Island, Western Australia, serial sections; *Conus boholensis* Petuch, 1979 New Caledonia; *Conus fragillisimus* Petuch, 1979 Port Sudan, serial sections; *Conus taeniatus* Hwass, 1792 Port Sudan, serial sections; *Conus textile* Linnaeus, 1758 Seychelles, serial sections; *Conus ventricosus* Gmelin, 1791; **Raphitominae**: *Phymorhynchus moscalevi* Sysoev & Kantor, 1995, Mid-Atlantic Ridge. In addition all material cited by Taylor *et al.*, (1993) and Kantor *et al.*, (1997) was examined.

RESULTS

Examination of the teeth on the early part of the developing radular membrane in different species possessing wishbone teeth shows that, despite great variability in the shape of the fully formed teeth, the process of tooth 'maturation' is very similar. The most instructive examples are the radulae of *Comitas* spp., *Cochlespira* spp. and *Xenuroturris cingulifera*. The mature marginal teeth of these species are strikingly different in appearance. In *Comitas* spp. (Fig. 2c, e) they are broad and flat, with two obviously thickened borders, in *Cochlespira* spp. (Fig. 3c, e) they are slender with a very narrow accessory limb, while in *Xenuroturris* (Fig. 3h) the marginals are robust, with a wide base and very narrow accessory limb. However, in each species the immature teeth on the early parts of the radular membrane are closely similar in appearance.

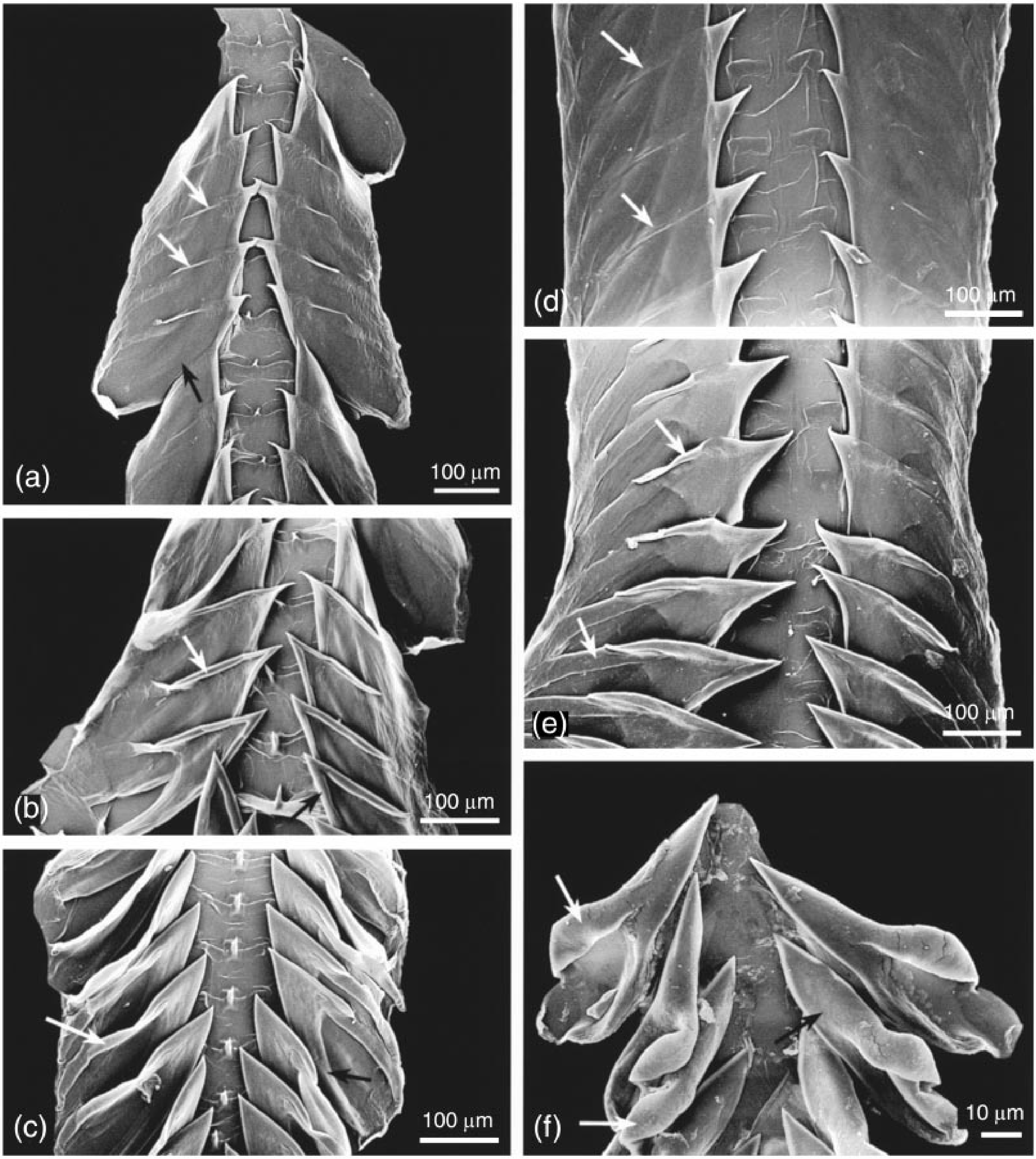

Fig. 2. Development of radulae in Turridae, subfamilies Cochlespirinae (a–e) and Turrinae (f). (a–c) *Comitas murrawolga* (Garrard, 1961). (a) The initial part of radula. (b). The 11–14th rows of forming teeth. (c) Fully formed teeth in the middle part of the radular membrane. (d–e) *Comitas onokeana vivens* Dell, 1956. (d) 7–10th rows of teeth. (e) 18–24th rows of teeth. (f) *Lophiotoma acuta* (Perry, 1811), the first three rows of teeth. White arrows indicate the forming accessory limbs and black arrows the major elements of the marginal teeth.

Fig. 3. Development of radulae in Turridae, subfamilies Cochlespirinae (a–e) and Turrinae (f–h). (a–d) *Cochlespira radiata* (Dall, 1889). (a) 4–9th rows of teeth. (b) 14–19th rows of forming teeth. (c) Fully formed teeth in the middle part of the radular membrane. (d) Enlarged marginals of 20–23rd rows. (e) *Cochlespira pulchella* (Schepman, 1913), enlarged, completely formed marginals. (f–h) *Xenuroturris cingulifera* (Lamarck, 1822). (f) Half row of newly formed teeth. Arrows indicate the non-thickened edge. (g) Semi-mature teeth. Note the commencement of lengthwise folding of the teeth. (h) fully matured teeth. White arrows indicate the forming accessory limbs and black arrows the major elements of the marginal teeth.

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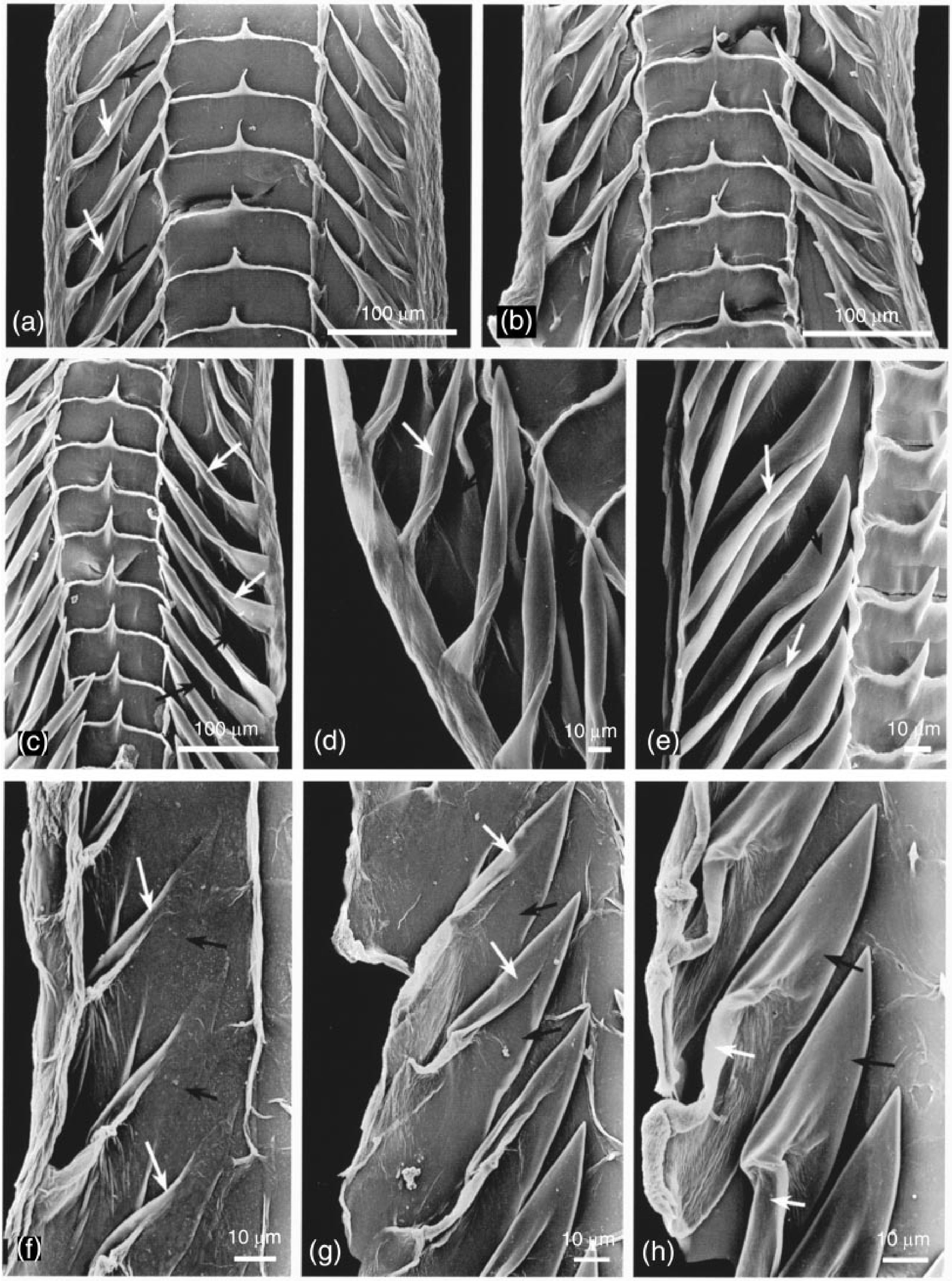
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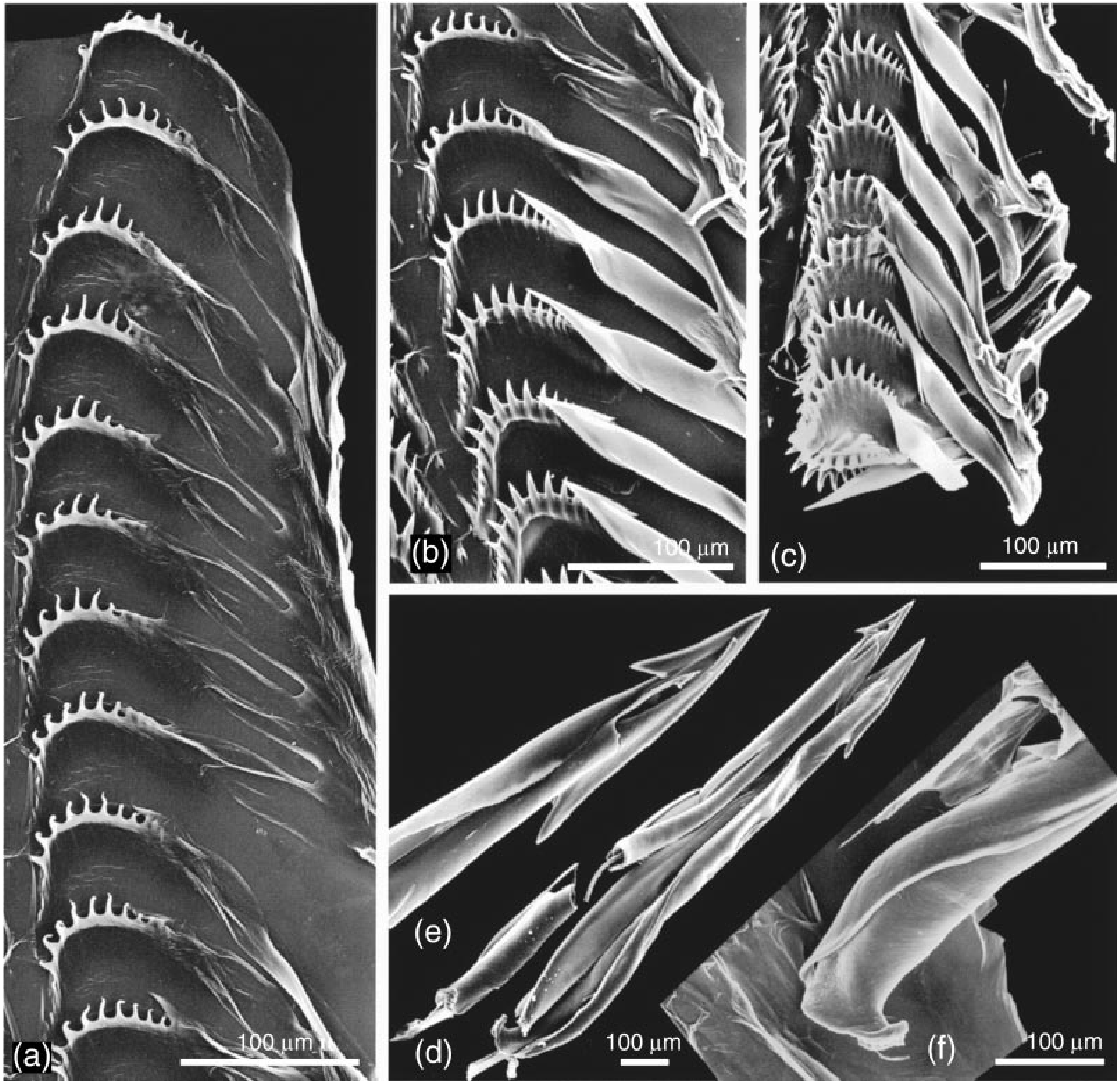

Fig. 4. (a–c) Development of the radula of *Imaclava pilsbryi* (Bartsch, 1950) (Clavidae). (a, b) Successive rows of forming teeth. Note the complete thickening of the marginals and its lengthways scrolling in (b). (c) Bending plane of the same radula. (d–f) *Toxiclionella tumida* (Sowerby, 1870) (Turridae, Clavatulinae). (d) Pair of completely formed hypodermic teeth. (e) Tip of the tooth, showing two barbs. (f) Base of the tooth with part of the subradular membrane.

In *Comitas murrawolga* (Fig. 2a–c) observations of the earliest part of the radular membrane show that the marginal teeth are initially formed as thin, flat plates, sometimes with barely visible borders. Gradually the margins of the plate thicken (Fig. 2b), while the plate itself folds longitudinally so that the posterior (youngest) edge elevates from the radular membrane (Fig. 2c). A similar process can be seen in *Comitas onokeana vivens* (Fig. 2d, e). Maturation of a different kind of marginal tooth is seen in *Cochlespira radiata* and *C. pulchella* (Fig. 3a–e). Again the posterior edge, which forms the accessory limb, gradually thickens and elevates from the radular ribbon, twisting to overlie the major limb (Fig. 2d,e). The maturation process is also similar in *Xenuroturris cingulifera* (Fig. 3f–h). Initial thickening of the posterior edge (Fig. 3f) forms the accessory limb which elevates from the radular membrane, twists slightly and comes to overlie the later maturing major limb, which forms the distal tip and blade of the tooth. In all the examples it is clear from the photographs that the 'major element' of the tooth is attached to the subradular membrane along nearly its whole length, while the 'accessory limb' is not a separate element but, in fact, represents the free thickened

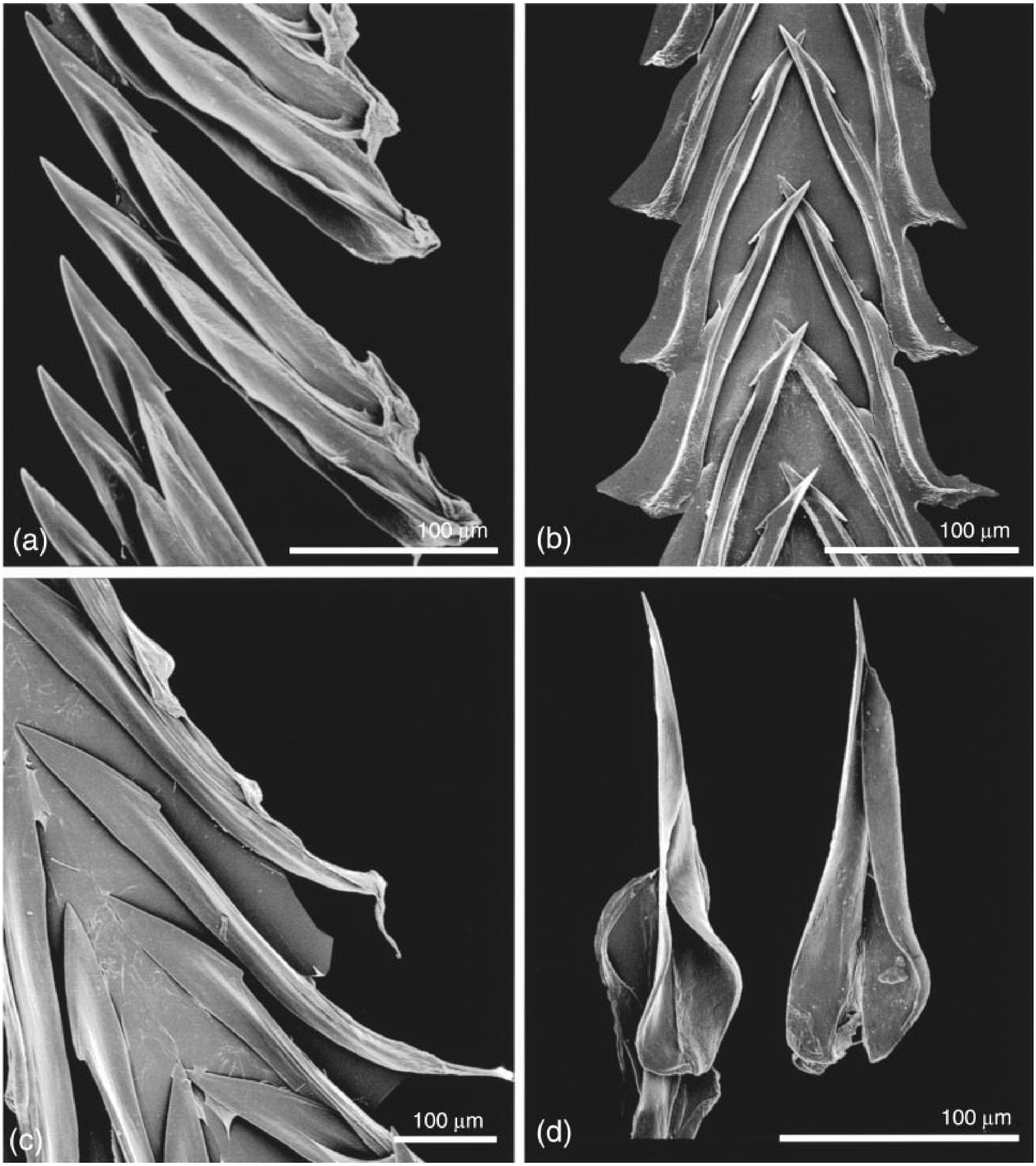

Fig. 5. (a) Semi-enrolled teeth of *Pilsbryspira nympha* (Pilsbry & Lowe, 1932) (Turridae, Zonulispirinae). (b) Flat teeth with slightly thickened margins of *Cheungbeia robusta* (Hinds, 1843) (Turridae, Crassispirinae). (c) Flat teeth with thickened outer margins of *Funa jeffreysii* (Smith, 1875) (Turridae, Crassispirinae). (d) Hollow and awl-shaped teeth of *Ptychobela suturalis* (Gray, 1838) in different stages of unfolding (Turridae, Crassispirinae).

margin of the tooth that elevates in the process of tooth sclerotization. In fully formed teeth, the unthickened central part of the tooth can be very thin and is often invisible with light microscopy, thus creating the illusion that the limbs are separated from each other (as in many published drawings of these teeth).

The rate of tooth maturation can vary greatly among different species. While in *Comitas murrawolga* the teeth of rows 11–12 are already more or less sclerotized, in *C. onokeana vivens* they remain poorly defined for the first 22 rows. In *Cochlespira radiata* the edges of the teeth become thickened by rows 5–6, but remain practi-

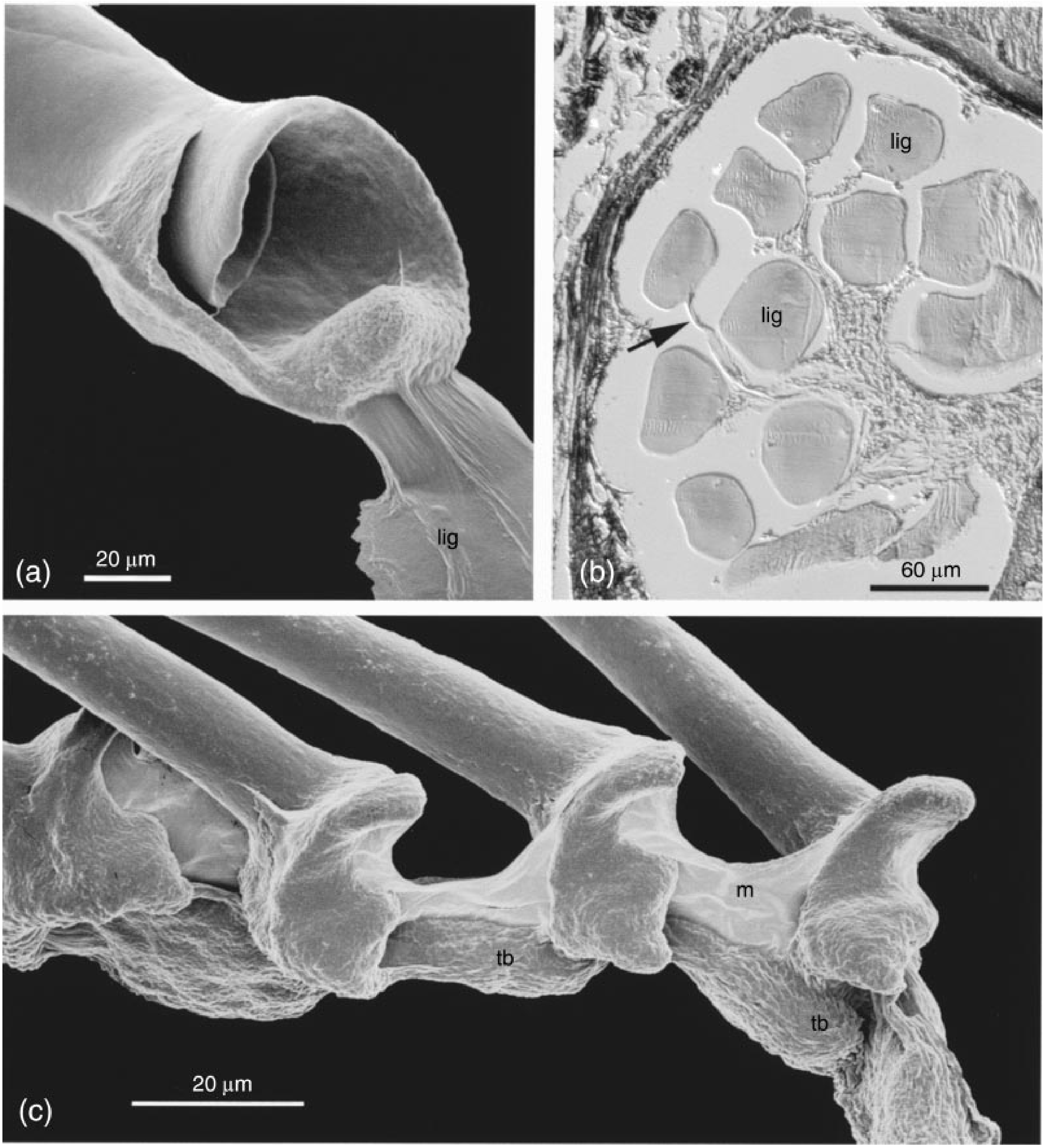

Fig. 6. (a) Base of enrolled tooth of *Conus ventricosus* Gmelin, 1791 showing ligament. (b) Section of radular sac of *Conus textile* Linnaeus, 1758 showing tooth ligaments attached to thin membrane (arrowed). (c) Lateral view of teeth of *Phymorhynchus moscalevi* Sysoev & Kantor, 1995 showing teeth joined at bases by a thin membrane. Abbreviations: lig, ligament; m = radular membrane; tb = extended tooth base.

cally unfolded for the first 20–22 rows, before reaching their more or less final shape. In *Xenuroturris cingulifera*, although the maturing teeth remain non-sclerotized for some distance, sclerotization then occurs rather sharply and the teeth attain their final shape within rows 4–5. In species with robust marginal teeth, such as *Lophiotoma acuta* (Fig. 2f) and *Clionella sinuata*, only the very first row of teeth resembles a more or less flat plate, which has almost the shape of the mature tooth, while in the second row the accessory limb is already raised and the teeth are indistinguishable in shape from those that are fully mature. The 'semi-enrolled' marginal teeth found in the subfamily Zonulispirinae, e.g. *Pilsbryspira nympha* (Fig. 5a) are probably formed in a similar manner. Sclerotization of the free, unattached margin is much less pronounced and therefore the fully formed tooth attains an evenly rounded shape.

In those species having enrolled marginal teeth and also a robust radular membrane, the process of tooth maturation is similar to that described for duplex teeth. In *Imaclava pilsbryi*, for example, which has five teeth in each row, the mature marginal teeth are loosely enrolled with a small barb (Fig. 4c). Observations of the maturing teeth show the sequence of development of the enrolled teeth. At the earliest stages the tooth is an elongate, flat plate (Fig. 4a); the posterior edge then thickens and elevates from the radular membrane (Fig. 4a, b) while the anterior edge remains attached. The posterior edge subsequently curves over and twists, forming a scroll-like tube with only slight overlap of the edges (Fig. 4b), while the distal edge thickens to form the blade and barb of the tooth (Fig. 4c). *Toxiclionella tumida* (Fig. 4d–f) also possesses enrolled, barbed teeth which are firmly attached to the radular ribbon along their lengths. In section the teeth are seen as loosely enrolled, with only slight overlapping of the tooth edges (Fig. 4d–f). Due to lack of suitable material our observations of the maturing teeth were limited, but it is likely that development is similar to that of *Imaclava pilsbryi*.

Although we were unable to study the maturation of the hollow marginal teeth of the Conidae with SEM, observations of thin sections through the radular sac showed that the scroll-like teeth are enrolled at first formation, confirming Bergh's (1896) observations, although the very first pair of teeth may be more loosely enrolled than later ones. Conids are generally thought to lack a continuous radular membrane, however, our thin sections through the radular sacs of several species (*Conus anemone*, *C. fragillisimus*, *C. taeniatus*, *C. textile* and *Borsonia ochracea*, revealed a very thin membrane joining the tooth ligaments to each other (Fig. 6a, b). This membrane is a remnant of the radular ribbon. This reduced membrane is also seen in the raphitomine *Phymorhynchus moscalevi* in which the teeth are linked to each other at their bases (Fig. 6c).

Within the subfamily Crassispirinae (Turridae) there is a great diversity in the shape of marginal duplex teeth (Kantor *et al*., 1997). While the majority of species show normal duplex teeth, some species have flat teeth, with only a narrow thickened zone along the free margin of the tooth (*Vexitomina garrardi, Funa* spp., Fig. 5c). Others are flat with both margins distinctly thickened (*Cheungbeia* spp., Fig. 5b). Finally, there are the awl-shaped teeth of *Ptychobela suturalis* (Fig. 5d), in which both edges of the tooth are detached from the membrane and overlap each other, so that the a hollow tube is formed in the pointed anterior part of the tooth but which broadens and opens posteriorly. In this case the tooth is attached to the membrane only along a narrow central zone. In only one case, *Hindsiclava militaris* (Reeve, 1843), have we observed the apparent complete detachment of the accessory limb in the central part of a tooth (Kantor *et al*., 1997: fig. 14a). We cannot exclude the possibility that this is an artifact, caused by the cleaning or air-drying of the radula, whereby the thin cuticle of the central part of the tooth has been damaged or dissolved.

A simplified summary diagram of transverse sections through the middle part of the major types of marginal teeth examined in this study is given in Fig. 7.

DISCUSSION

We have demonstrated that duplex marginal teeth, as found in many species of Turridae, are a single, blade-shaped unit with thickened edges, and that there is no separation between the two thickened limbs as previously thought. Shimek & Kohn's (1981) initial observation of the formation of the secondary limb from thickening of the tooth edge has been confirmed and extended to more species. Study of the maturation of teeth along the radular membrane shows that widely different morphologies of duplex teeth are formed in a similar way by thickening of the tooth edges, longitudinal folding and progressive elevation of the posterior edge of the tooth from the membrane. These observations of the mode of maturation or sclerotization of duplex teeth demonstrate that, in the initial stages, this type of tooth is rather similar to the simple, flat teeth of some Clavidae, such as *Drillia rosacea* (Taylor *et al*., 1993: fig. 20a). The enrolled and semi-enrolled teeth of *Imaclava*, *Pilsbryspira* and *Toxiclionella* are also formed in a similar way, with the length of the tooth remaining attached to the radular ribbon and the edges curving over and slightly overlapping each other (Fig. 7). At present we cannot say whether the simple form of the teeth in *Vexitomina, Funa* and *Cheungbeia* (Fig. 5b, c) represent the initial stages of formation of the 'normal' duplex tooth, or if it is secondary simplification. According to our previous phylogenetic analysis (Kantor *et al*., 1997) species with the 'normal' duplex tooth constitute the sister taxa for these genera suggesting that the simple teeth represent a derived state.

The thickening of the margins of duplex teeth, folding along the length and partial enrolling can be explained as features which provide mechanical strength. Although the use of hollow, enrolled, hypodermic teeth at the proboscis tip for piercing and envenomation of prey is well known in *Conus* and other Conidae (Kohn, 1990; Olivera *et al*., 1990), we have previously demonstrated that most types of conoidean radular teeth, including flat plates and duplex forms, may also be used at the proboscis tip (Sysoev & Kantor, 1987, 1989; Kantor & Taylor, 1991). In fact this mode of prey capture has been demonstrated for all groups of Conoidea possessing a venom gland and radula, excepting the Pseudomelatomidae. In mechanical terms, it is well known from beam theory that a simple flat plate is less stiff and more likely to buckle when subject to a compressive force, than one with thickened edges or

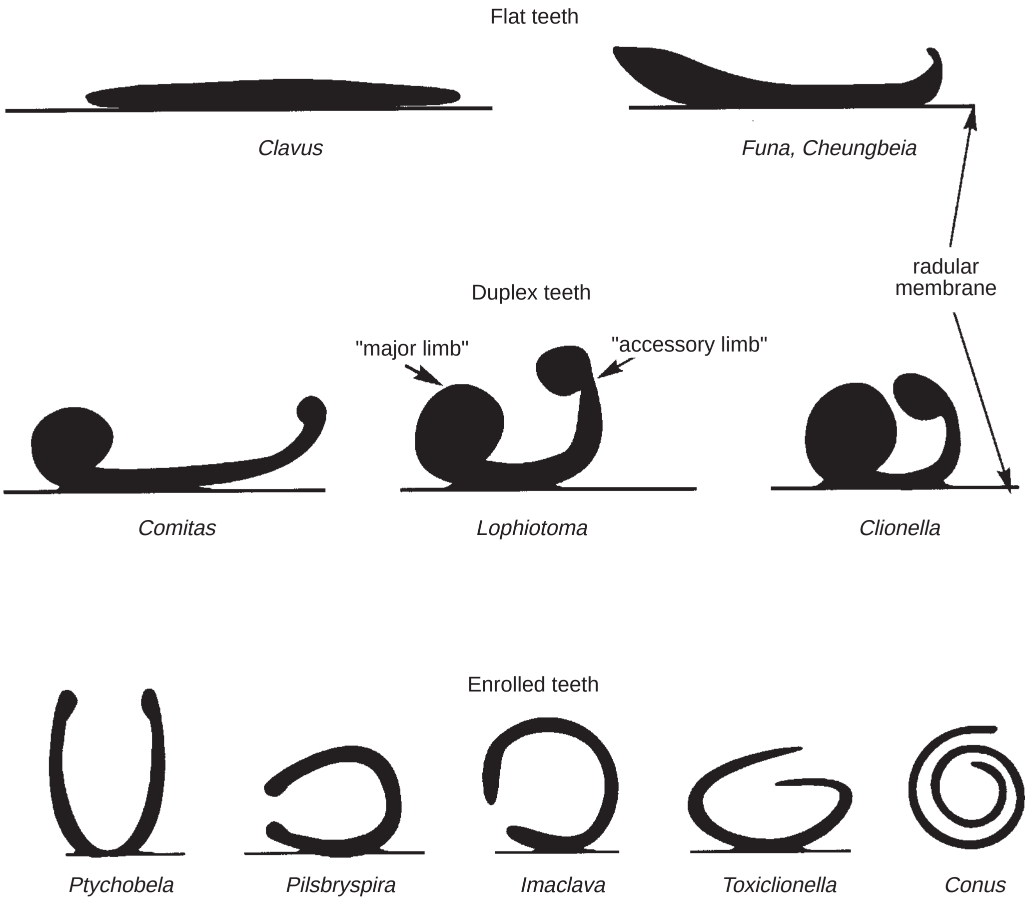

Fig. 7. Summary diagram showing transverse sections (mid-tooth) of the main types of marginal radular teeth mentioned in this study. Only in *Conus* is the tooth free from the radular membrane except for the basal ligament.

a hollow cylinder (Wainwright *et al.*, 1976). With this in mind, we propose as an explanation that the transformations of the marginal teeth in conoideans have been driven by the requirement to strengthen the tooth without adding more material to it, thereby increasing its effectiveness during stabbing and penetration of the prey. Both the thickening of tooth edges and folding, which are seen to different degrees amongst the duplex teeth of Turridae, probably increase the strength and stiffness of the tooth, thereby reducing the possibility of bending and buckling. The distal tips of the teeth are pointed, with blade-like edges for penetration of the epidermis of the prey. The groove between the 'limbs' of the duplex tooth may possibly function to channel venom to the tip of the tooth. Shimek & Kohn (1981) suggested the different types of duplex teeth were used in the buccal cavity after the prey have already been ingested. In fact, it appears that marginal teeth when still attached to the membrane can hardly be functional, for they are attached along most of their length, with only the tips elevated slightly at the bending plane of the radula. This suggests that the transformations and elaborations of the teeth are more likely adaptations for their use once deployed at the proboscis tip, subsequent to their detachment from the membrane. It is also interesting that teeth that are never used at the proboscis tip (Type 2 see above) are attached to the radular ribbon only by their rather narrow bases and are free along most of their length. Therefore, when the radula passes over the bending plane the teeth are raised and fully functional (Kantor, 1988, fig. 1F).

The most important trend in the evolution of the conoidean radula is the formation of hollow, enrolled marginal teeth, with the various elaborations of the distal tips into blades and barbs (Fig. 1d). These teeth can be very effective in venom delivery, penetrating deeply into the body wall of the prey, with the venom passing down the hollow tooth and out of a channel at the tip. The increased stiffness resulting from the enrolling of the marginal teeth also enables them to grow longer, thereby probably making attacks more effective with deeper penetration into the prey and even, as in some *Conus*, the holding of prey with the tooth. Indeed, comparison of the relative sizes of the marginal teeth show a clear tendency for enrolled teeth to be longer when compared with flat or duplex teeth. In Crassispirinae (Kantor *et al.*, 1997) tooth length represents 0.3% (*Crassispira maura*) to 1.3% of shell length (*Cheungbeia mindanensis)*, in Cochlespirinae 0.4% (*Cochlespira radiata*) to 0.7% (*Comitas murrawolga*), and about 2% for the enrolled teeth of *Toxiclionella tumida* (Clavatulinae). In the family Conidae, the teeth are larger still and frequently represent more than 1% of shell length and up to 5% in *Oenopota harpa* (Sysoev, 1983). In

Conus, the smallest tooth recorded comprises 0.7% (*Conus chaldeus*), but most are around 2.5–4%, with the longest teeth found amongst the mollusc feeders such as *Conus textile* (10–15% of shell length) (James, 1980; Kohn *et al*., 1999; Nishi & Kohn, 1999).

In those species in which the radular teeth are attached to the radular membrane along their length (family Turridae) any changes of tooth shape during their maturation are produced by the supraradular epithelium. The epithelium acts in one direction only, up and down, allowing lifting and bending of the tooth edges. This explains why even enrolled teeth are formed by no more than one turn of the enrolled tooth plate (Fig. 7).

The most important difference between the radulae of Conidae (s.l.) and Turridae is that in the former the teeth are not attached to a membrane but are free along their length. Although Taylor *et al*. (1993) considered that a continuous radular ribbon is absent in the family Conidae, Shimek & Kohn (1981) mentioned, without giving details, that species with hypodermic teeth have a vestigial membrane. Beck (1996: fig. 6) illustrated in *Phymorhynchus hyfifluxi* (Conidae, Raphitominae) that the bases of the teeth were linked by some sort of membrane. Our observations of *Phymorhynchus moscalevi* and other conids (Fig. 6b, c) show that a membrane is present but the teeth are attached only at their bases by a more or less long ligament. Examination of the sections through the radular sac showed that the very first teeth are already enrolled and the teeth can be formed by several turns as in *Conus* (Fig. 7). This becomes possible because the teeth are surrounded by secretory epithelium which can act in all directions. This also allows more elaboration of the tooth into barbs and spurs. Alpers (1931) mentioned that the teeth of *Conus lividus* are initially formed flat and then became enrolled by the action of the supraradular and subradular epithelia. We cannot prove or disprove these observations at present but it is possible that tooth formation in Conidae may differ slightly between groups. Nevertheless, the most important fact is that the tooth is enrolled from a flat plate.

It is suggested that one of the main reasons for the shift of place of attachment of the tooth in Conidae is to remove any limitations on the transformation of the hypodermic tooth allowing a high degree of enrollment. Hitherto, we had considered that the reduction of the membrane was for reasons of redundancy, because the radula does not function as a whole organ in species with hypodermic teeth.

With the loss or reduction in the radular membrane and rearrangement of the radula, the radular caecum (or short arm of the radular sac), a modification of the sublingual pouch, becomes an important structure. In Conidae it functions as a storage sac, analogous to an archer's quiver, for holding radular teeth prior to their use at the proboscis tip. Our phylogenetic analyses demonstrate that the transformation of the sublingual pouch into radular caecum has occurred independently in the Terebridae and Conidae (Taylor *et al*., 1993).

Taylor *et al*. (1993) suggested that the basic morphological differences between the foreguts of Turridae and Conidae are the absence of the radular membrane and the presence of the radular caecum in the latter. Although this study has shown that the membrane is present in at least in some Conidae (if not all) there is an important difference in radular morphology, that is, the mode of attachment of the teeth to the membrane.

In conclusion, we have demonstrated that the different types of marginal teeth found in conoideans are formed in a similar way. Contrary to our preconceptions there is not a large difference between duplex teeth and hypodermic teeth, either in terms of ontogeny or function. Since most of the different forms of teeth can be used at the proboscis tip for stabbing and envenomating the prey, it is no surprise that the hollow, hypodermic teeth may have evolved independently in different clades of conoideans, since selection should favour more efficient penetration of the prey and venom delivery. Thus, enrollment of the teeth provides mechanical stiffness, while the hollow cylinder allows precise localized delivery of the venom to the site of incision into the prey, whether polychaete, mollusc or fish. Although clades of Turridae possessing various forms of duplex teeth are diverse and often abundant, the most speciose clades of conoideans are those with hypodermic teeth (Sysoev, 1991).

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