

Unified terminology for cestode microtriches: a proposal from the International Workshops on Cestode Systematics in 2002–2008

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Abstract: Terminology for microtriches, the surface features both unique to and ubiquitous among cestodes, is standardised based on discussions that occurred at the International Workshops on Cestode Systematics in Storrs, Connecticut, USA in 2002, in České Budějovice, Czech Republic in 2005 and in Smolenice, Slovakia in 2008. The following terms were endorsed for the components of individual microtriches: The distal, electron-dense portion is the *cap*, the proximal more electron-lucent region is the *base*. These two elements are separated from one another by the *baseplate*. The base is composed of, among other elements, *microfilaments*. The cap is composed of *cap tubules*. The electron-lucent central portion of the base is referred to as the *core*. The core may be surrounded by an electron-dense *tunic*. The entire microthrix is bounded by a *plasma membrane*, the external layer of which is referred to as the *glycocalyx*. Two distinct sizes of microtriches are recognised: those ≤ 200 nm in basal width, termed *filitriches*, and those >200 nm in basal width, termed *spintriches*. Filitriches are considered to occur in three lengths: *papilliform* (≤ 2 times as long as wide), *acicular* (2–6 times as long as wide), and *capilliform* (>6 times as long as wide). In instances in which filitriches appear to be doubled at their base, the modifier *duplicated* is used. Spintriches are much more variable in form. At present a total of 25 spinithrix shapes are recognised. These consist of 13 in which the width greatly exceeds the thickness (i.e., *bifid*, *bifurcate*, *cordate*, *gladiate*, *hamulate*, *lanceolate*, *lineate*, *lingulate*, *palmate*, *pectinate*, *spathulate*, *trifid*, and *trifurcate*), and 12 in which width and thickness are approximately equal (i.e., *chelate*, *clavate*, *columnar*, *coniform*, *costate*, *cyrillionate*, *hastate*, *rostrate*, *scolopate*, *stellate*, *trullate*, and *uncinate*). Spiniiform microtriches can bear marginal (*serrate*) and/or dorsoventral (*gongylate*) elaborations; they can also bear apical features (*aristate*). The latter two modifiers should be used only if the features are present. The terminology to describe the overall form of a spinithrix should be used in the following order: tip, margins, shape. Each type of microthrix variation is defined and illustrated with one or more scanning electron micrographs. An indication of the taxa in which each of the microthrix forms is found is also provided.

Key words: microthrix, microtriches, Cestoda, ultrastructure, tegument

The monophyly of the cestodes is a concept that is now generally accepted, and has become relatively widely known. Less well known, however, is the fact that the monophyly of this class of platyhelminths is supported by a remarkably distinctive surface feature, unique to cestodes, often referred to as the *microthrix*. In addition to being unique to cestodes, microtriches appear to be ubiquitous among cestodes. They have now been reported from representatives of all cestode orders. They are present in the adult forms of all cestode species examined to date. They have also been reported from the earlier life-cycle stages of many cestode species. Not unexpectedly, with this taxonomic breadth has come a diversity of terminologies applied somewhat inconsistently among microthrix forms across different taxa and life-cycle stages. Discussions aimed at standardising microthrix terminology began at the 4th International Workshop on Cestode Systematics in Storrs, Connecticut in 2002, continued at the 5th International Workshop on Cestode Systematics

and Phylogeny in České Budějovice, Czech Republic in 2005, and were concluded at the 6th International Workshop on Cestode Systematics in Smolenice, Slovakia, in 2008. This paper describes the terminology resulting from those discussions, adopted by the participating members of the global community of Cestodologists. This is the third in a series of papers aimed at standardising cestode terminology resulting from discussions at the International Cestode Workshops (see also Chervy 2002, Conn and Świdorski 2008).

Goals of this paper

The primary goals of this paper were to develop a standardised terminology for (1) the components of individual microtriches, (2) the two basic types of microtriches, and, perhaps most importantly, (3) the diversity of forms of the two basic types of microtriches exhibited by cestodes.

In order to maximise the utility of the new terminology, its development was based on microthrix variation seen

across as wide a taxonomic spectrum of cestodes as possible. To achieve this, an extensive survey was made of the literature. In addition, a number of specimens were examined *de novo* with scanning electron microscopy (SEM). We strove for a terminology that was descriptive, yet simple, but also flexible, in the hope that it could readily accommodate microthrix forms beyond those seen to date, because clearly much microthrix variation remains to be discovered. Our efforts were guided to some extent by similar efforts to standardise descriptors of morphological features in other taxonomic groups (e.g., Anonymous 1962, Clopton 2004). Brown (1956) and Borror (1960) served as rich sources of candidate terms to describe microthrix forms. It is our hope that this standardised microthrix terminology will serve to enhance the significance and predictive powers of comparative studies across cestode taxa, from both functional and phylogenetic standpoints.

History

Structures ornamenting the surfaces of cestodes were first observed in the 19th century. In the earliest reports, these features were described as “fibrilles protoplasmiques” (Sommer and Landois 1872), “Cilien” (Schiefferdecker 1874, Steudener 1877), “fibres” (Moniez 1881), or as “fine rods or threads” (Leuckart 1886). Descriptions of these structures early in the first half of the 20th century were somewhat more detailed (e.g., Goldschmidt 1900, Pratt 1909, Young 1908, Coutelen 1927, Rietschel 1935, Crusz 1947), with some studies including discussions of the development and/or the possible functions of these features. Hyman (1951; p. 320) described the outermost layer of the “cuticle” of cestodes as consisting of “a comidial layer...which is fringe-like and may be extended into fine hairs, spines, or scales”. In the first study to present results from transmission electron microscopy (TEM) of the cestode tegument, Read (1955) reported “villus-like structures” on the surfaces of immature proglottids of both *Raillietina cesticillus* Molin, 1858 and *Hymenolepis diminuta* Rudolphi, 1819. He suggested these structures might maintain an intimate relationship with the mucosal surface and postulated that they might serve an absorptive function. Shortly thereafter, a number of additional authors observed these structures in a diversity of tapeworm taxa. For example, Kent (1957) reported and provided TEM images of “micropapilles” in several cyclophyllidean species, which he envisioned might engage between intestinal villousities. Rundell (1957) observed structures he referred to as “comidia” on the surfaces of five species of cyclophyllideans and one proteocephalidean. Rees (1958; p. 470) described “closely set, backwardly projecting structures which have been variously named ‘pseudocilia’, ‘cirri’, or ‘hairs’” on the surface of the bothriocephalideans *Bothriocephalus scorpii* Müller, 1776 and *Clestopothrium crassiceps* (Rudolphi, 1819).

However, it was Rothman (1959) who, also employing TEM methods, argued convincingly for the unique nature of these cestode structures, proposing the terms microthrix (s.) and microtriches (pl.), and ultimately describing the various elements of these structures in some detail in 1963. Rothman (1963) was also the first to address the full spectrum of possible functions these structures might perform. Following quickly on the heels of Rothman’s work, were investigations of these surface features in the adult and/or metacestode stages (*sensu* Chervy 2002) of a variety of other gyrocotylideans (Lyons 1969), caryophyllideans (e.g., Béguin 1966), diphyllbothriideans (e.g., McCaig and Hopkins 1965, Bråten 1968a, b, Charles and Orr 1968, Yamane 1968), trypanorhynch and tetraphyllideans (e.g., Lumsden 1966), proteocephalideans (e.g., Threadgold 1964, 1965) and cyclophyllideans (e.g., Waitz 1961, Rosario 1962, Voge 1962, 1963, Siddiqui 1963, Howells 1965, Race et al. 1965, Lumsden 1966, Morseth 1966, 1967, Baron 1968, Lumsden et al. 1968), with many of these studies also employing TEM. Although Rothman’s terms were not immediately universally adopted (e.g., for alternatives see Béguin 1966, Lee 1966, Morseth 1966), by the end of that same decade, they had essentially become the standards. Similarly, the ubiquity of microtriches among cestodes was generally accepted, as were their remarkable differences in form among taxa, life-cycle stages, and regions of the body. Much progress had also been made towards the characterisation of the microarchitecture of microtriches (e.g., Bråten 1968a, Lyons 1969, Morris and Finnegan 1969). For example, the universality of their bipartite nature, consisting of a distal electron-dense region and a proximal electron-lucent region, despite the variety in form, had been firmly established. In 1969, Jha and Smyth provided a detailed account of microthrix structure and proposed formal terminology for some of the major components of individual microtriches.

Berger and Mettrick (1971) were the first to employ methods of SEM to explore the surface features of cestodes. Their work on the microtriches of the cyclophyllideans *Hymenolepis diminuta* (Rudolphi, 1819) and *Hymenolepis nana* (Rudolphi, 1819) provided a new perspective on microthrix form. They confirmed the existence of two distinct types of microtriches (i.e., a “short tubular form” and a “long flattened form”). Later that decade, papers describing two (or in some instances possibly more) types of microtriches appeared with some regularity as a result of work conducted using TEM and/or SEM in caryophyllideans (e.g., Hayunga and Mackiewicz 1975), a spathebothriidean (Burt and Sandeman 1974), diphyllbothriideans (e.g., Kwa 1972, Grammelvedt 1973, Lumsden et al. 1974, Andersen 1975, Yamane et al. 1975), trypanorhynch (Lumsden 1975a, Halton and McKerr 1979), and also in bothriocephalideans (e.g., Timofeev and Kuperman 1972, Jones 1975, Boyce

1976, Andersen 1979), tetraphyllideans (McVicar 1972, Gabrion and Euzet-Sicard 1979) and other cyclophyllideans (e.g., Jha and Smyth 1971, Featherston 1972, 1975, Blitz and Smyth 1973, Rees 1973, Euzet and Gabrion 1976, Hess and Guggenheim 1977, Hulinská 1977a, b, 1978, Gabrion and Euzet-Sicard 1979, Voge et al. 1979); an account of an unusual form in a lecanicephalidean also appeared early in the decade (e.g., Rifkin et al. 1970). Of note among works that decade was McVicar's (1972) detailed account of the close association between the microtriches of several tetraphyllideans and the microvilli of the spiral intestine of their host. Lumsden also provided comprehensive reviews of microthrix structure and, in particular, function (Lumsden 1975a, b).

In their seminal 1980 paper, Thompson et al. fully characterised the microtriches on the scolex of the proteocephalidean *Kapsulotaenia tidswelli* (Johnston, 1909). These authors adopted much of the terminology of Jha and Smyth (1969) for the specific components of microtriches. Based on extensive TEM work, they presented a detailed account of the structural and dimensional differences seen in microtriches among different regions of the scolex and strobila. They recognised several different varieties of filamentous microtriches (e.g., short or with a terminal membranous bleb) and also several different forms of robust microtriches (i.e., blade-like, spine-like, and peg-like) depending on the region of the scolex, neck, and strobila examined. They also provided insights into the different functions each of these forms might perform. They further demonstrated that some scolex structures that had previously been interpreted to be spines were, in fact, large microtriches.

The 1980's also saw the generation of SEM images of microtriches on the external surfaces of metacestodes and/or adults of additional species of bothriocephalideans (e.g., Pool and Chubb 1985), proteocephalideans (e.g., Coggins 1980, Jilek and Crites 1980) and cyclophyllideans (e.g., Valkounová and Prokopič 1980, Hulinská 1981, Czaplinski et al. 1988, Gijon-Botella et al. 1989), but also for the first time of amphilinideans (e.g., Rohde and Georgi 1983, Rohde 1986), haplobothriideans (e.g., Thomas 1983, MacKinnon et al. 1985), diphyllideans (e.g., Probert and Stobart 1989), and tetrabothriideans (e.g., Andersen and Lysfjord 1982). Some remarkable microthrix morphologies were observed in tetraphyllideans (Whittaker and Carvajal 1980, McCullough and Fairweather 1983, Whittaker et al. 1985, Caira and Pritchard 1986), and trypanorhynch (Whittaker et al. 1982, 1985, McCullough and Fairweather 1983, Shields 1985, Andersen 1987, Carvajal et al. 1987, Hildreth and Lumsden 1987). However, TEM work continued, often also revealing unusual microthrix forms, on the various external surfaces of metacestodes and/or adults of caryophyllideans (Richards and Arme 1981a, b, Poddubnaya et al. 1986), haplobothriideans (MacKinnon and Burt 1985a, b, MacKinnon et

al. 1985), diphyllbothriideans (Park et al. 1981, Yamane et al. 1982a, b, 1989, Ishii et al. 1988, Andersen and Gibson 1989), bothriocephalideans (e.g., Tedesco and Coggins 1980, Jarecka et al. 1981, Granath et al. 1983) and cyclophyllideans (Hulinská and Lavrov 1981, Mehlhorn et al. 1981, Schramlová and Lavrov 1981, Gabrion 1982, MacKinnon and Burt 1983, Novak and Dowsett 1983, Czaplinski et al. 1984, 1988, Holy and Oaks 1986, Conn 1988, Harris et al. 1989, Mizinska-Boevska et al. 1989).

The first studies aimed at determining the nature of the spine-like structures on the tegument lining elements of the reproductive system of cestodes began to appear that same decade. For example, using TEM, Beveridge and Smith (1985) convincingly demonstrated the presence of microtriches both in the vagina and on the cirrus of the tetraphyllidean *Phyllobothrium vegans* Haswell, 1902; they also noted having seen similar structures in a cyclophyllidean and a proteocephalidean. Similarly, Jones (1989) provided a detailed description of at least two different types of microtriches on the cirrus of the cyclophyllidean *Cylindrotaenia hickmani* (Jones, 1985).

In a classic TEM study, Holy and Oaks (1986) summarised the micro-architecture of microtriches in elegant detail and made several specific recommendations for the terminology applied to the individual components of these structures. For example, they noted that, based on their structure and composition, the cytoskeletal filaments in the base should be termed microfilaments, rather than microtubules, as they had been termed by some previous authors (e.g., Smyth 1969). Holy and Oaks (1986; fig. 20) also generated the most detailed and informative schematic illustration of a reconstruction of a microthrix available to date.

Kuperman (1980) provided a thoughtful analysis of the systematic significance of microtriches among cestodes. In one of the most comprehensive contributions to microthrix literature, based on extensive TEM and SEM work, Kuperman (1988) provided the first detailed treatment of microthrix form in a diphyllidean and spathebothriidean, and also for a diversity of bothriocephalidean, caryophyllidean, and trypanorhynch taxa. Furthermore, several reviews provided insights into the structure and function of microtriches in the model organism *Hymenolepis diminuta* (e.g., Lumsden and Specian 1980, Threadgold 1984), and in cestodes more generally (e.g., Lumsden and Murphy 1980, Halton 1982, Lumsden and Hildreth 1983, Smyth and McManus 1989).

Several extensive reviews treating the structure and/or possible functions of microtriches appeared early in the 1990's (e.g., Coil 1991, Hayunga 1991). However, the microthrix literature of that decade was dominated by papers employing SEM methods to characterise microtriches on the scolices of a wide array of taxa. In fact, the characterisation of scolex microtriches became a regular component of the descriptions of new cestode species. Taxa

(novel or known) for which SEM data were generated included caryophyllideans (e.g., Poddubnaya 1995, 1996, Lyngdoh and Tandon 1996), diphyllbothriideans (Nishiyama et al. 1993, Tsuboi et al. 1993), trypanorhynch (Richmond and Caira 1991, Palm 1995, 1997, Jones and Beveridge 1998, Palm et al. 1998, Campbell et al. 1999, Casado et al. 1999), diphyllideans (Ivanov and Campbell 1998a, Tyler and Caira 1999), tetraphyllideans (Caira 1990a,b 1992, Caira and Ruhnke 1990, 1991, Ruhnke 1993, 1994a, b, 1996a, b, Caira and Orringer 1995, Caira and Keeling 1996, Caira et al. 1996, Nasin et al. 1997, Ivanov and Campbell 1998b, McKenzie and Caira 1998), lecanicephalideans (e.g., Brockerhoff and Jones 1995), proteocephalideans (Hanzelová et al. 1995, Rego et al. 1999, Scholz et al. 1999), tetrabothriideans (e.g., Hoberg et al. 1995), and cyclophyllideans (e.g., Davydov et al. 1990, Irshadullah et al. 1990, Ashour et al. 1994, Casado et al. 1994, Cielecka et al. 1994, Bâ et al. 1995, Fourie et al. 1997). In an interesting TEM study, Biserova (1991), working with the diphyllidean *Echinobothrium typus* van Beneden, 1849, recognised two distinct types of microtriches. She used the term “polymicrothrix” for complex multidigitate forms of the larger microthrix type, and “microthrix” for all simple forms of microtriches. Within polymicrotriches, she distinguished between those of type 1 (with three digits) and type 2 (with greater than three digits).

Among other trends, these works confirmed that microthrix morphologies and/or distributions were consistent at a diversity of taxonomic levels (e.g., palmate microtriches restricted to some trypanorhynchs and diphyllideans; maiziform microtriches found only in a subset of tetraphyllidean genera including *Paraorygmatobothrium* Ruhnke, 1994, *Orygmatobothrium* Diesing, 1863, etc.). Based on extensive SEM of tetraphyllideans, Caira (1990b) advocated the systematic utility of scolex microtriches at least in onchobothriid tapeworms. As a result of SEM study of 27 taxa, Palm (1995) considered microthrix morphology to be of systematic utility in trypanorhynchs, particularly at the generic and specific levels. Recommendations for the standardisation of the regions of the scolex from which SEM images are routinely obtained were made for trypanorhynchs (e.g., Richmond and Caira 1991, Palm 1995) and tetraphyllideans (e.g., Caira 1990b, Caira et al. 1999, 2001). Caira et al. also provided a taxonomically comprehensive analysis of microthrix variation across cestode taxa, coding 23 SEM microthrix characters for 63 species in six cestode orders in 1999, and for 127 species in nine orders in 2001.

However TEM work also continued that decade with detailed information being provided on spathebothriideans (e.g., Davydov et al. 1997), diphyllbothriideans (e.g., Yazaki et al. 1990), bothriocephalideans (e.g., Davydov et al. 1995, Diaz-Castañeda et al. 1995, Žďárská and Nebesářová 1997), proteocephalideans (e.g., Žďárská and Nebesářová 1999), cyclophyllideans (e.g., Seif 1992,

Grytner-Zięcina et al. 1995), and amphilinideans (e.g., Davydov and Kuperman 1993).

The present decade has seen the generation of SEM data and/or in some instances also TEM data for microtriches in an even wider array of cestode taxa once again, especially in the context of the description of new species. Taxa examined have included additional gyrocotylideans (Poddubnaya et al. 2006), caryophyllideans (Poddubnaya 2003b, Poddubnaya et al. 2003), spathebothriideans (Marques et al. 2007, Poddubnaya 2007, Levron et al. 2008c), diphyllbothriideans (Chubb et al. 2006), diphyllideans (e.g., Faliex et al. 2000, Neifar et al. 2001, Tyler 2001, Ivanov and Lipshitz 2006, Twohig et al. 2008), trypanorhynchs (e.g., Beveridge and Jones 2000, Jones 2000, Palm 2000, Palm et al. 2000, Beveridge and Campbell 2001, Palm and Schröder 2001, Palm, 2008), bothriocephalideans (Poddubnaya, 2003a, Gil de Perterra and Semenas 2005, 2006, Poddubnaya et al. 2007, Kuchta and Scholz 2008, Kuchta et al. 2008a, b, 2009, Levron et al. 2008a), cyclophyllideans (e.g., Stoitsova et al. 2001), lecanicephalideans (Ivanov and Campbell 2000, Jensen 2001, 2005, 2006), the first litobothriideans (Olson and Caira 2001), and the first cathetocephalideans (Caira et al. 2005).

However, figuring particularly prominently in this literature were the proteocephalideans (e.g., Bruňanská et al. 2000, Gil de Perterra and de Chambrier 2000, Cañeda-Guzmán et al. 2001, de Chambrier 2001, 2003, 2004, 2006, de Chambrier et al. 2003, 2004, 2005, 2006a, b, 2007, 2008, 2009a, b, Gil de Perterra 2002, 2004, 2005, 2009, Žďárská and Nebesářová 2003, 2005, Žďárská et al. 2004, Arredondo and Gil de Perterra 2008, de Chambrier and Scholz 2008, Scholz et al. 2008) and the tetraphyllideans and rhinebothriideans (e.g., Caira and Burge 2001, Ghoshroy and Caira 2001, Caira and Zahner 2001, Caira and Tracy 2002, Ivanov and Brooks 2002, Ivanov and Campbell 2002, Healy 2003, 2006a, b, Caira et al. 2004, 2005, 2007a, b, Ivanov 2004, 2005, 2006, 2008, Agusti et al. 2005, Caira and Durkin 2006, Fyler and Caira 2006, Jensen and Caira 2006, 2008, Reyda and Caira 2006, Ruhnke and Thompson 2006, Ruhnke et al. 2006a, b, Reyda 2008, Ruhnke and Carpenter 2008, Twohig et al. 2008, Menoret and Ivanov 2009).

In addition, several monographs focusing on specific cestode orders provided SEM data for the microtriches of a substantial number of species and/or genera. In his monograph on the trypanorhynchs, Palm (2004) presented one or more SEM image of microtriches on the scolices of over 50 species representing a wide array of trypanorhynch families; he also provided TEM images to illuminate interpretation of some of the more interesting microthrix forms seen in certain members of this order. In their respective monographs, Jensen (2005) presented SEM images of exemplars of 11 lecanicephalidean genera, and Tyler (2006) provided SEM images of a total of 14 species in both genera of diphyllideans. In their revision of

the bothriocephalideans, Kuchta et al. (2008b) presented SEM images of 27 species representing 27 genera.

Much headway was also made investigating the existence and nature of microtriches on the terminal genitalia of cestodes including bothriocephalideans (e.g., Poddubnaya 2003a, Levron et al. 2008b, Poddubnaya and Mackiewicz 2009), diphyllbothriideans (e.g., Poddubnaya 2002a, b), spathebothriideans (e.g., Poddubnaya et al. 2005a, b, 2007), and rhinebothriideans and tetraphyllideans (e.g., Reyda 2008).

Over half a century of work on the surface elaborations of cestodes has enhanced our understanding of these features to the point that standardisation of the terminology applied to these features is now in order. The term “microvillus” has been used in a number of different contexts in reference to the surface features of cestodes. In some cases, this term has been applied to structures that truly lack an electron-dense distal portion (e.g., MacKinnon and Burt 1984, Holcman and Heath, 1997). However, in other instances, the term has been applied to features that have actually been demonstrated to possess an electron-dense distal portion (e.g., Lee 1966, Holy and Oaks 1986), or, although examined only with SEM, likely possess an electron-dense distal portion (e.g., Whittaker et al. 1982). While some similarities exist between microvilli and microtriches, the distinctions between these two types of structures have been described in detail by a number of authors (e.g., Lumsden and Hildreth 1983, Holcman and Heath 1997). The structure of microtriches, most specifically their possession of an electron-dense cap, makes them unique among the cellular surface elaborations seen in animals. Thus, we believe these structures are justifiably referred to with the unique term *microthrix* (pl. *microtriches*).

(1) Terminology for the components of a microthrix

Fig. 1

The bipartite nature of microtriches, each consisting of a distal, electron-dense portion and a proximal, relatively electron-lucent portion, was recognised early in the literature. A diversity of terms has been used to describe the distal portion. These have included “tip” (e.g., Threadgold 1965), “spine” (Lee 1966), “spike” (e.g., Morseth 1967), “cap” (e.g., Charles and Orr 1968), “apex” (e.g., Mackiewicz 1972), and “shaft” (e.g., Jha and Smyth 1969), with the latter term gaining much popularity after the detailed treatment of Jha and Smyth (e.g., Hess and Guggenheim 1977, Coggins 1980, Thompson et al. 1980, Whittaker and Carvajal 1980, Granath et al. 1983, MacKinnon and Burt 1983, Beveridge and Smith 1985, Seif 1992). Terminology applied to the proximal, electron-lucent portion of a microthrix has been less variable, consisting primarily of “base” (e.g., Threadgold 1965) and “shaft” (e.g., Lee 1966). Unfortunately, the latter term also gained some popularity (e.g., Richards and Arme 1981a, Lumsden and

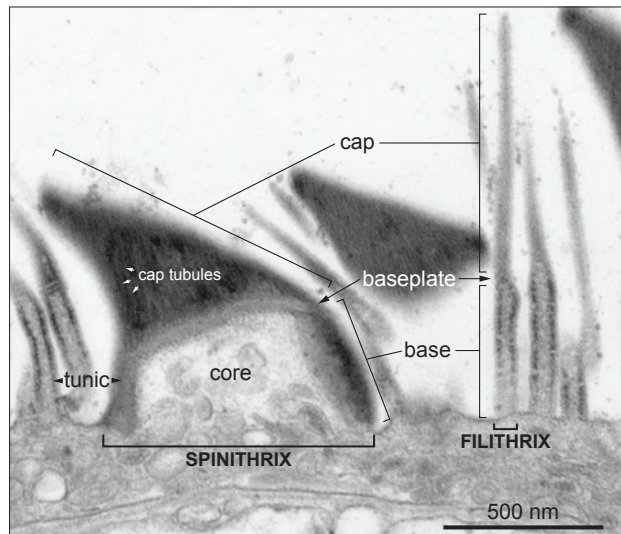


Fig. 1. Standardised terminology proposed for components of microtriches (filitriches and spinitriches). TEM through proximal surface of bothridium of *Calliobothrium* cf. *verticillatum* (Rudolphi, 1819). Note: base microfilaments and glycocalyx not shown.

Hildreth 1983, Threadgold and Dunn 1983, Threadgold 1984, Hildreth and Lumsden 1987, Smyth and McManus 1989, Lyngdoh and Tandon 1996), which has led to confusion with the same term having now been applied to both portions of a microthrix. The feature located at the boundary between the distal and proximal portions of a microthrix has been referred to as an “electron-lucid zone” (Threadgold 1965), a “tube-like structure” (e.g., Jha and Smyth 1969), a “junctional region” (e.g., Holy and Oaks 1986), and a multilaminar “baseplate” (e.g., Lumsden et al. 1974), with the latter term gaining some popularity (e.g., Hess and Guggenheim 1977, Thompson et al. 1980, Lumsden and Hildreth 1983, Richards and Arme 1984).

The terminology endorsed here for the components of a microthrix are summarised in Fig. 1. This terminology is generally consistent with that presented by Levron et al. (2008a). The distal, electron-dense portion of a microthrix should be referred to as the *cap* and the proximal, electron-lucent region should be referred to as the *base*. This avoids the issues associated with the dual application of the term “shaft” and is consistent with the terms for these regions applied by Holy and Oaks (1986) in their detailed treatment of microthrix architecture. We propose use of the term *baseplate* for the structure located at the boundary of the base and the cap. This term is in common use and is the simplest of the terms that have previously been applied to this feature. Following Holy and Oaks (1986), the filaments of the base should be referred to as *microfilaments*. The most appropriate term for the structures constituting the cap is more problematic for their identity in the realm of the cytoskeleton as microtubules, interme-

diate filaments (i.e., keratin filaments), or microfilaments (i.e., actin-containing filaments) remains to be elucidated (J. Oaks, pers. comm.). However, as it has been shown that they are not actin-based (Holy and Oaks 1986), they should not be referred to as microfilaments (e.g., Levron et al. 2008a). In the interim, it would seem most appropriate to refer to them merely as *cap tubules*. For simplicity, we propose that the electron-dense sheath surrounding the electron-lucent *core* of the base should be referred to as a *tunic*, rather than a “core tunic” as suggested by Holy and Oaks (1986). The entire microthrix, including both the base and cap, is bounded by a *plasma membrane*, the external carbohydrate layer of which is termed the *glycocalyx* (not visible in Fig. 1).

(2) Terminology for two basic microthrix types

Fig. 1

There is general consensus that, across cestode taxa, body regions, and developmental stages, microtriches commonly occur in two basic forms: a larger, more robust form, and a smaller, more slender form. Unlike the larger, more robust form, which can range, for example, from 0.33 μm in width in *Paraberrapex manifestus* Jensen, 2001 (see Jensen 2001) to over 6.6 μm in width, for example in *Yorkeria izardi* Caira, Jensen et Rajan, 2007 (see Caira et al. 2007a), the basal width of the smaller, more slender form appears to be rather conserved across taxa. Examples of reported ranges in the basal width of the more slender form include 0.12–0.19 μm in *Hymenolepis diminuta* (see Rothman 1963, Lumsden and Specian 1980, Threadgold 1984), 0.1 μm in two species of *Diphyllobothrium* Cobbold, 1858 (see Yamane 1968), 0.1 μm in *Gyrocotyle urna* (Wagener, 1852) (see Lyons 1969), 0.2 μm in *Raillietina cesticillus* (see Baron 1971), 0.08–0.09 μm in *Mesocestoides corti* Høeppli, 1925 (see Hess and Guggenheim 1977), 0.166 μm in *Caryophyllaeus laticeps* (Pallas, 1781) (see Richards and Arme 1981b), 0.12–0.16 μm in *Bothriocephalus acheilognathi* Yamaguti, 1934 (see Granath et al. 1983), 0.12 μm in *Haplobothrium globuliforme* Cooper, 1914 (see Thomas 1983), 0.12 μm in *Phyllobothrium vagans* Haswell, 1902 (see Beveridge and Smith 1985), 0.1 μm in *Taenia taeniaeformis* (Batsch, 1786) (see Bortoletti and Ferretti 1985), 0.1 μm in two species of *Fimbria* Froelich, 1802 (see Grytner-Zięcina et al. 1995), 0.1 μm in *Bombycirhynchus sphyranaeicum* (Pintner, 1930) (see Palm et al. 1998), ~0.1 μm among cestodes in general (Caira et al. 1999, 2001), 0.065–0.167 μm in *Calliobothrium* cf. *verticillatum* (Rudolphi, 1819) (see Fyler 2007). In fact, Fyler (2007) presented statistical evidence that a significant difference exists in the average basal width between the smaller, more slender microthrix form and the larger, more robust microthrix form in *Calliobothrium* cf. *verticillatum*.

Thus, with respect to a formal criterion that can be objectively applied to distinguish the smaller, more slender

microthrix form from its larger, more robust counterpart, we propose that 0.2 μm (i.e., 200 nm) is an appropriate threshold base width. Options for the terms that might be applied to the two forms are many, and varied. For example, Berger and Mettrick (1971) referred to them as “conical” and “spathulate”, Andersen (1975) as “slender” and “conical”, Featherston (1975) as “slender and filamentous” and “broader spikes”, Hess and Guggenheim (1977), Hess (1980), and Thompson et al. (1982) as “blade-like” and “filamentous”, Gabrion and Euzet-Sicard (1979) as “lanceolated” and “filamentous”, Voge et al. (1979) as “blade-shaped or conical” and “elongated slender” and, Kuperman (1988) as “tubular” and “cone-shaped”, Caira and Ruhnke (1990) as “spiniform microtriches” and “filiform microtriches” with one or both of the latter terms gaining some popularity throughout the 1990’s (e.g., Ruhnke 1994a, 1996b, Ivanov and Campbell 1998b). Faliex et al. (2000) subsequently proposed that the latter terms be contracted as “spinithrix” and “filithrix”, respectively. In the interest of developing as streamlined a terminology as possible, we propose formal adoption of *spinithrix* (pl. *spinitriches*) and *filithrix* (pl. *filitriches*) following Faliex et al. (2000). Thus, microtriches with basal widths of ≤ 200 nm should be considered to be *filitriches*; those with basal widths > 200 nm should be considered to be *spinitriches*.

(3) Terminology of filithrix and spinithrix forms

Figs. 2–9

Filitriches, and especially spinitriches, come in a wide variety of forms. This variation is most pronounced among major cestode taxa, but, as noted above, it has also been observed among regions of the body (in particular among regions of the scolex) and among developmental stages within individual species. Unfortunately, the terminology applied to describe variation in microthrix form has not kept pace with the discovery of microthrix variation. As a consequence, microthrix terminology has become somewhat unwieldy as terms have proliferated, and have been applied inconsistently across microthrix forms and cestode taxa. The terminology described below was designed to begin to remedy this situation.

It should be noted that the proposed terminology emphasises data generated from SEM over TEM. This is because, in the absence of relatively large numbers of serial sections, microthrix form is very difficult to assess using TEM alone. Interpretation of form can vary depending on the angle of the section taken; in many cases, the specifics of a form (e.g., the distribution of marginal and/or dorso-ventral projections) are impossible to determine without the aid of SEM. In addition, perhaps because SEM is faster and easier to employ than TEM, SEM data are currently available for a much broader spectrum of taxa than are TEM data. Thus, the terminology proposed here does not take into account internal microthrix features such as the

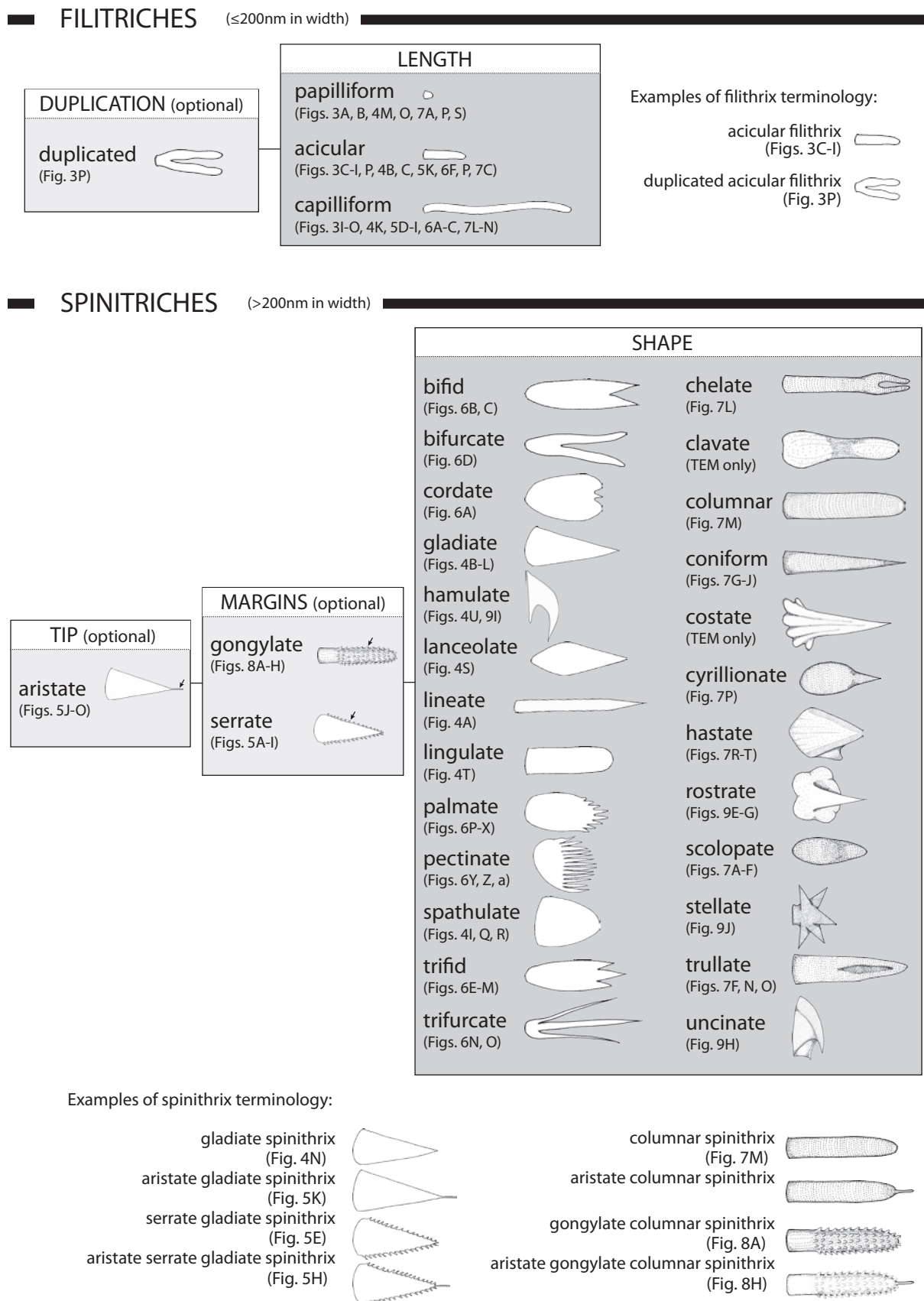


Fig. 2. Schematic representation of terms proposed to describe filitrix (upper panel) and spinitrix (lower panel) forms. Dark grey boxes indicate mandatory descriptors; lighter grey boxes indicate those used only when applicable.

extent of the electron-dense cap or the configuration of the electron-dense tunic (if any) surrounding the core, both of which have been shown with TEM to vary somewhat among taxa (e.g., Palm 2004). Nonetheless, it is our hope that TEM data will ultimately be generated for the variety of microthrix forms articulated below, providing additional information to test the circumscription of these forms.

With respect to illustrating the proposed terminology, we have taken two different approaches. Fig. 2 summarizes this terminology and serves as a quick reference to facilitate application of these terms. This figure presents schematic representations of the three conditions of filithrix length, and the 25 spinithrix shapes, and their apical (tip) and marginal and/or dorsoventral modifications. It also illustrates several examples of the application of these terms. In addition, SEM images illustrating as much of the proposed terminology as possible are provided in Figs. 3–9. In most cases, we have provided multiple examples of each form in order to illustrate what we consider to be acceptable variation within a particular form. However, to conserve space, Fig. 2 refers to only subsets of the SEM images in Figs. 3–9.

FILITHRIX TERMINOLOGY

(applied to microtriches with basal widths of ≤ 200 nm)

Figs. 2, 3

Historically, only a few authors have gone beyond acknowledging the existence of filitriches, to recognising specific forms of filitriches. Thus, only a few terms exist as options to adopt for describing variation in filithrix form. Nonetheless, much confusion exists in the application of the limited array of available terms. In many cases the term “filiform” appears to have been used to refer to the more elongate filithrix form (e.g., Hoberg et al. 1995, de Chambrier et al. 2008, 2009a, b, de Chambrier and Scholz 2008), which appears to be the most commonly encountered and ubiquitous form. Following examination of multiple litobothriidean, cathetocephalidean, diphyllidean, trypanorhynch, rhinebothriidean, and tetraphyllidean taxa, Caira et al. (1999, 2001) recognised two distinct forms of filitriches, short and long, distinguishing between these two forms on the basis of whether their length was equal to, or greater than, their basal width. These authors employed the terms “short filiform microthrix” and “long filiform microthrix,” respectively to these two forms. Hoberg et al. (1995) referred to a “papilliform” microthrix, which appears to be consistent with the short filiform microthrix of Caira et al. (1999, 2001). The term “small filiform microthrix” has been used to describe filitriches seen in proteocephalideans (e.g., de Chambrier et al. 2008) and bothriocephalideans (e.g., Kuchta et al. 2008a, 2009). However, examination of the images of the latter authors suggests that this form may actually be intermediate in length between the shortest and longest forms seen by previous authors such as

Hoberg et al. (1995) and Caira et al. (1999). Palm (2004) provided the most detailed treatment of filithrix forms to date. He presented four terms for referring to filitriches, depending on a combination of filithrix length and extent of the electron-dense cap. These forms consisted of “papillate”, “aciculate”, “capilliform”, and “filiform”.

In general, variation in filithrix form is relatively straightforward when compared to that seen among spinitriches. Filitriches vary primarily in length. The terminology proposed here accommodates the three basic filithrix lengths observed to date. The fact that some filitriches bear pointed tips and others bear rounded tips has not been incorporated into the proposed terminology. Also not incorporated at this time is the degree of flexibility exhibited by filitriches; some are consistently stiff (e.g., Fig. 3F), whereas others are remarkably flexible (e.g., Fig. 3M). In the cases of both tip form and degree of flexibility, this is because we believe that the extent of the electron-dense cap may have a bearing on these aspects of filithrix form, and are thus hesitant to develop a terminology to accommodate these types of variation in the absence of more extensive TEM data. As a consequence, while we have adopted some elements of the terminology of Palm (2004), we have not endorsed all elements. In addition, the forms of the terms used here deviate somewhat from those of Palm (2004), so as to be more correct with respect to their derivation from Greek or Latin. So, for example, we have modified the term papillate (L., covered with papillae) to papilliform (L., shaped like a papilla), etc. The proposed terminology also recognises the fact that filitriches can be duplicated, or even in rare cases, triplicated, at their bases.

I. Filiform microthrix length

(i) Papilliform (shaped like a papilla) (*papilla*; L., nipple)

Figs. 2, 3A, B, 4M, O–R, 6H, X–Z, a, 7A, P, S

This is the shortest of the filithrix forms. This term applies to filitriches that are up to two times as long as they are wide. That these minute structures represent true microtriches, a fact assumed by Caira et al. (1999), was convincingly demonstrated by Fyler (2007), who provided detailed evidence from TEM that they possess all of the elements (e.g., electron-dense cap, etc.) of true microtriches. These structures are typical, for example, of the distal bothridial surfaces of multiloculate onchobothriid tetraphyllideans (e.g., Caira 1990b, Fyler and Caira 2006, Reyda and Caira 2006); they have also been observed in a diversity of trypanorhynchs (e.g., Palm 2004).

(ii) Acicular (shaped like a small pin) (*acicula*; L., small pin, needle)

Figs. 2, 3C–I, P, 4B, C, J, N, T, 5K, 6F, P–S, V, W, 7C, G, K, Q, R, T

This term applies to filitriches that are >2 to 6 times as long as they are wide. These structures have been found, for example, on the distal bothridial surfaces of a diver-

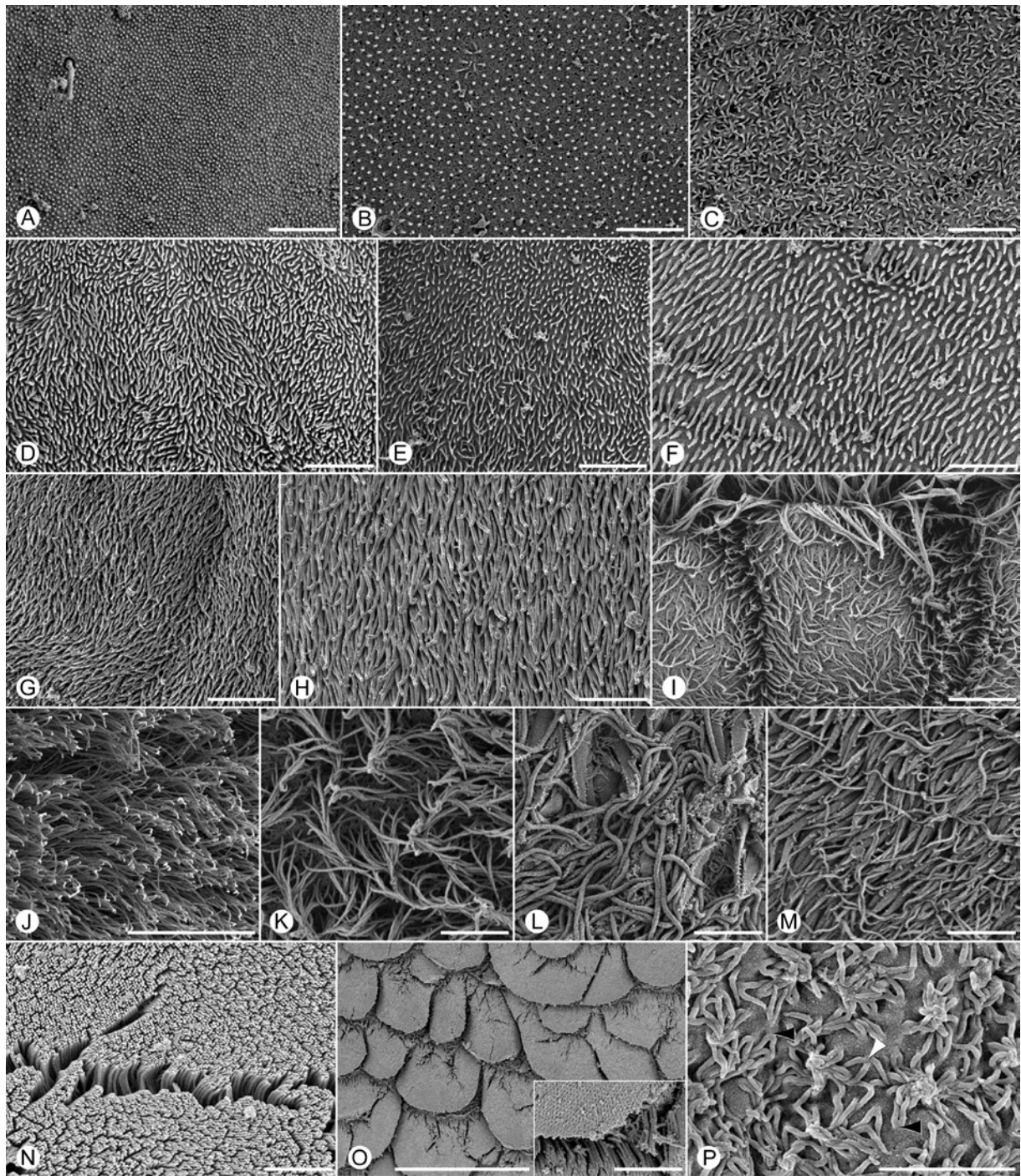


Fig. 3. Scanning electron micrographs illustrating filitriches. **A** – Distal bothridial surface of *Acanthobothrium marymichaelorum*; **papilliform filitriches**. **B** – Apical region anterior to hooks of bothridium of *Yorckeria garneri*; **papilliform filitriches**. **C** – Anterior region anterior to hooks of bothridium of *Yorckeria garneri*; **acicular filitriches**. **D** – Distal bothridial surface of *Anthocephalum centrurum*; **acicular filitriches**. **E** – Proximal surface of bothridial apical sucker of *Anthocephalum centrurum*; **acicular filitriches**. **F** – Lacination of proglottid of *Litobothrium janovyi*; **acicular filitriches**. **G** – Scolex proper of *Lecanicephalum* sp.; **acicular filitriches**. **H** – Distal region of scolex of *Caryophyllaeus laticeps*; **acicular filitriches**. **I** – Proximal surface of bothridial marginal loculus of new tetraphyllidean genus from *Himantura pastinacoides*; **acicular** and **capilliform filitriches**. **J** – Strobila of *Cyathocephalus truncatus*; **capilliform filitriches**. **K** – Apical region of bothridium anterior to hooks of *Megalonychos sumansinghai*; **capilliform filitriches**. **L** – Distal bothridial surface of *Orygmatobothrium* sp.; **capilliform filitriches** and **serrate spinitriches**. **M** – Proximal surface of sucker of *Proteocephalus perplexus*; **capilliform filitriches** and **coniform spinitriches**. **N** – Strobila of *Anthocephalum cairae*; **capilliform filitriches**. **O** – Strobilar scutes of *Orectolobicestus tyleri*; inset detail shows scutes composed of **capilliform filitriches**. **P** – Fourth cruciform pseudosegment of *Litobothrium janovyi*; **duplicated acicular filitriches** (black arrowhead) and **triplicated acicular filitriches** (white arrowhead). Scale bars: Figs. A–I, K–N, inset in O, P = 2 µm; Figs. J, O = 10 µm.

sity of tetraphyllideans (e.g., Ruhnke 1994a, Caira et al. 2007b), rhinebothriideans (e.g., Healy 2006a, b), litobothriideans (e.g., Olson and Caira 2001), and lecanicephalideans (e.g., Jensen 2005).

(iii) Capilliform (thread or hair-like in form) (*capillus*; L., hair) Figs. 2, 3I–O, 4K, 5A, B, D–I, L, N, O, 6A–C, E, K, L, T, U, 7H, L–N, U, 9A, C–H

This is the longest of the filitrix forms. This term is applied to filitriches that are >6 times as long as they are wide. However, in most cases, the length of this form of filitrix greatly exceeds six times its width. While all are <200 nm in diameter, there appears to be some variation in the width of this filitrix form in some taxa (e.g., *Orygmatobothrium*, Fig. 3L). This is the most commonly reported form of filitrix to date. It has, for example, been observed on various regions of the scolex in a diversity of tetraphyllideans (e.g., Caira et al. 1999, 2001), proteocephalideans (e.g., Scholz et al. 1999), and diphyllideans (e.g., Ivanov and Campbell 1998a). This is also the filitrix form seen throughout the strobila of most cestode species. Furthermore, as noted, for example, by Ruhnke (1994a), Ruhnke et al. (2006a, b), Ivanov (2008) and Ruhnke and Carpenter (2008), the “scutes” described on the “neck” and strobila of tetraphyllidean genera such as *Paraorygmatobothrium* Ruhnke, 1994, *Orectolobicestus* Ruhnke, Caira et al. 2006, and *Orygmatobothrium* Diesing, 1863, respectively, actually consist of dense arrangements of these filitriches (see Fig. 3O and corresponding inset).

The typical highly dense arrangement of filitriches, and of capilliform filitriches in particular, leaves much to be learned about the bases of these structures. While there are a number of instances in which no specific basal elaborations have been seen in capilliform filitriches (e.g., Fig. 3K), laterally extended bases have been observed in other instances (e.g., Fig. 9A).

II. Duplication

Duplicated (doubled at its base) Figs. 2, 3P

This term should be applied to identical filitriches that arise from a common base. This form is difficult to categorise correctly if the base is not visible. Although this appears to be a relatively rare condition, duplicated filitriches of the acicular type have been reported on the strobila of litobothriideans (e.g., Olson and Caira 2001, black arrowhead in Fig. 3P). In such instances we propose the use of the term “duplicated” prior to the term describing the length of the filitrix. However, given how unusual this condition appears to be, we propose that in the absence of use of this modifier, a microtrich should be assumed to be single. It is easy to envision multiples of greater than two filitriches occurring in some cestode taxa. In such cases, variations on this term should be employed. So, for example, instances of three filitriches arising

from a single base (e.g., white arrowhead in Fig. 3P) would be considered to be triplicated, and so on.

SPINITRICH TERMINOLOGY

(applied to microtriches with basal widths >200 nm)

Figs. 2–9

Owing to the much greater degree of morphological variation seen in spinitriches, a much greater number of terms has historically been employed to describe the diversity of spinitrix forms observed to date. Once again, however, these terms have not necessarily been uniformly applied and it has not been uncommon for several different terms to be proposed to describe the same spinitrix form, even by the same author. For example, triangular spinitriches were referred to as “spiniform microtriches” by Ghoshroy and Caira (2001), as “bladelike spinitriches” by Caira and Tracy (2002) and as “gladiate spinitriches” by Caira et al. (2007a, b). On many occasions, authors have adopted new terms as required to describe unusual morphologies they have encountered. So, for example, Halton and McKerr (1979) referred to the unusual, large multidigitate microtrich form seen in the trypanorhynch *Grillotia erinaceus* (van Beneden, 1849) as “palmate”. Thompson et al. (1980) recognised “peg-like”, “blade-like”, and “spine-like” variations of the larger microtrich type in the proteocephalidean they examined. Whittaker and Carvajal (1980) referred to the spinitriches seen in the tetraphyllidean *Orygmatobothrium musteli* (van Beneden, 1849) as having an “ear-of-corn” appearance. Caira et al. (1999) later formalised this concept with their use of the term “maiziform”. On only two occasions have sets of terms been proposed to describe the overall variation seen in spinitriches. Caira et al. (1999, 2001) developed a series of standard modifiers to describe variations in form of spinitriches. These consisted of “blade-like”, “serrate”, “maiziform”, “pectinate”, and “tridentate”. Similarly, in his monograph on trypanorhynchs, Palm (2004) provided a relatively detailed treatment of terminology of microtriches guided to some extent by the group discussion of microtrich forms that occurred at the 4th International Workshop on Cestode Systematics in Storrs, Connecticut, USA, and recognised spinitriches of the following forms: gladiate, serrate, pectinate, palmate, tricuspidate, mucronate, aristate, lingulate, and bifurcate. However, even these terms have not been used consistently.

The terminology presented here for spinitriches builds on the schemes of Caira et al. (1999, 2001) and Palm (2004), both originally developed primarily for microtriches observed in elasmobranch cestodes. However, the present work represents a much more thorough treatment in that it attempts to accommodate variation seen in microtriches across all major cestode taxa.

Our review of spinitrix form suggests that the variation seen to date may be captured in a series of three modifiers, one describing overall shape, one addressing

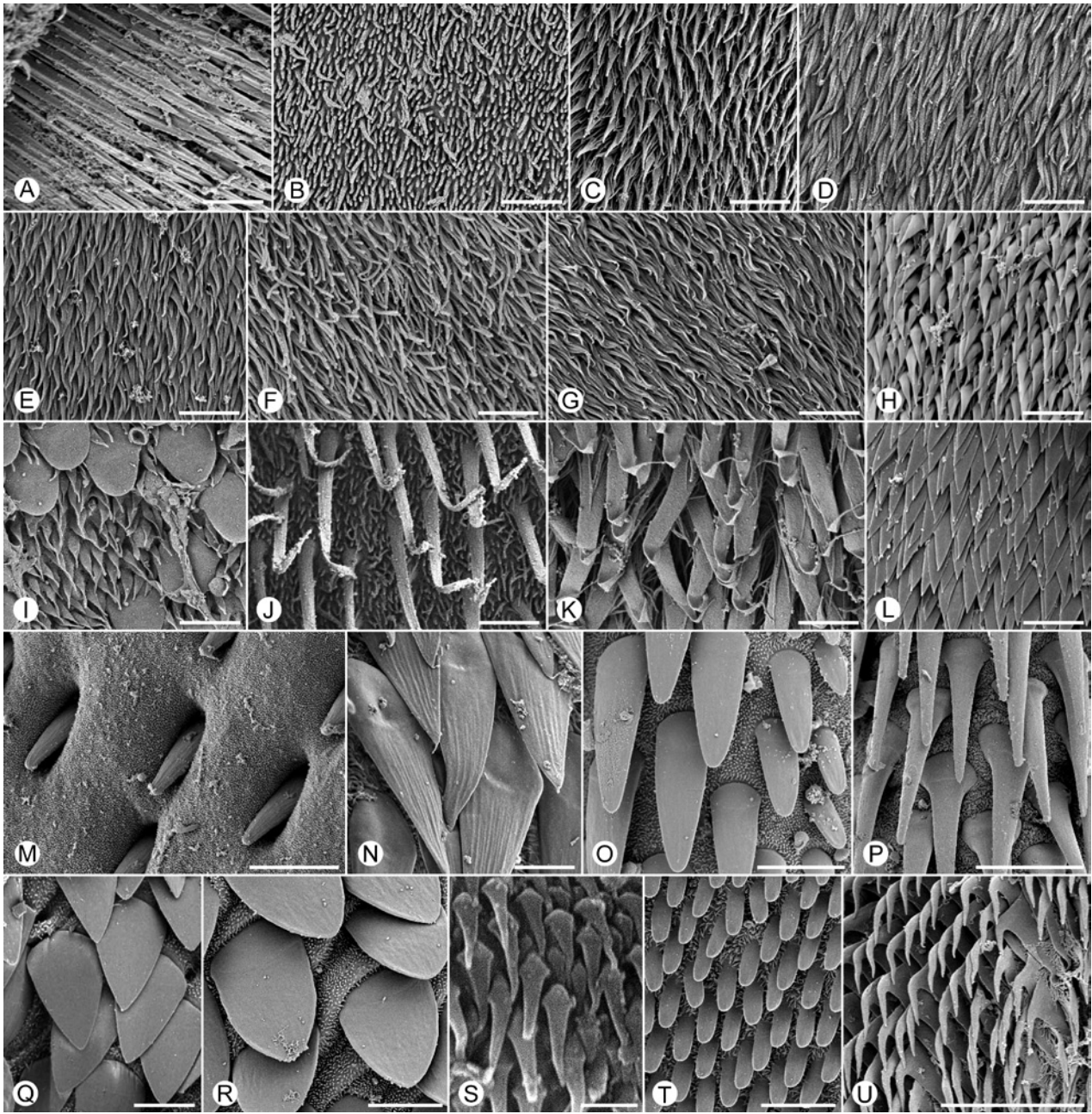


Fig. 4. Scanning electron micrographs illustrating some shapes of spinitriches in which width greatly exceeds thickness. **A** – Medial edge of distal bothrial surface of *Heteronybelinia estigmene*; **lineate spinitriches**. **B** – Lacination of fourth pseudosegment of *Litobothrium amplifica*; **small gladiate spinitriches** and **acicular filitriches**. **C** – Scolex proper of *Paraberrapex manifestus*; **small gladiate spinitriches** and **acicular filitriches**. **D** – Strobila of *Proteocephalus perplexus*; **small gladiate spinitriches**. **E** – Strobila of *Tetrabothrius cylindraceus*; **small gladiate spinitriches**. **F** – Distal region of scolex of *Khawia sinensis*; **small gladiate spinitriches**. **G** – Distal surface of sucker of *Echinococcus granulosus*; **small gladiate spinitriches**. **H** – Strobila of *Progynotaenia odhneri*; **gladiate spinitriches**. **I** – Distal acetabular surface of *Eniochobothrium euaxos*; **gladiate** and **spathulate spinitriches**. **J** – Proximal bothridial surface of *Ceratobothrium xanthocephalum*; **narrow gladiate spinitriches** and **acicular filitriches**. **K** – Distal surface of anterior of bothridial loculus of *Megalonychos sumansinghai*; **narrow gladiate spinitriches** and **capilliform filitriches**. **L** – Cephalic peduncle of *Erudituncus* sp.; **gladiate spinitriches**. **M** – Lateral region of proglottid of *Gastrolecithus planus*; **gladiate spinitriches** and **papilliform filitriches**. **N** – Pedicel of bothridial pair of *Yorckeria kelleyae*; **aristate gladiate spinitriches** and **acicular filitriches**. **O** – Proximal bothridial surface of *Yorckeria teeveeyi*; **gladiate spinitriches** and **papilliform filitriches**. **P** – Peduncle of *Phoreiobothrium lewinensis*; **gladiate spinitriches** and **papilliform filitriches**. **Q** – Pedicel of bothridial pair of *Yorckeria saliputum*; **spathulate spinitriches** and **papilliform filitriches**. **R** – Pedicel of bothridial pair of *Yorckeria izardi*; **spathulate spinitriches** and **papilliform filitriches**. **S** – Strobila of *Tetrabothrius lutzi*; **lanceolate spinitriches**. **T** – Distal surface of post-hook loculus in *Yorckeria izardi*; **lingulate spinitriches** and **acicular filitriches**. **U** – Margin of bothrium in *Heteronybelinia estigmene*; **hamulate spinitriches** and **capilliform filitriches**. Scale bars: Figs. A–L, N = 2 µm; Figs. M, U = 10 µm; Figs. O, Q, R, T = 5 µm; Fig. P = 20 µm; Fig. S = 1 µm.

marginal and/or dorsoventral elaborations, and one addressing apical features. Thus we have separated the description of apical and marginal and/or dorsoventral modifications, such as serrations, from the terms used to describe the form of the structure. We propose that these three sets of modifiers be used consistently, in the following sequence as appropriate: apical elaborations, marginal and/or dorsoventral modifications, and basic shape. Given their relative rarity, we suggest that the modifiers describing apical and marginal and/or dorsoventral modifications should be used only if applicable. Thus, in the absence of a marginal and/or dorsoventral modifier, a spinithrix should be considered to possess smooth margins. Similarly, a spinithrix should be assumed to lack an apical modification if the apical modifier is not used. We recognise 25 spinithrix shapes. In determining the appropriate term to apply to a shape, it is helpful to consider both the basic form and whether the width of a spinithrix greatly exceeds its thickness. In Fig. 2, those forms in which the width greatly exceeds the thickness are shown in the left column in the spinithrix shape panel and those forms in which the width is approximately equal to the thickness are shown in the right column in that panel. In the description of spinithrix forms that follows, forms in which width greatly exceeds thickness are presented first, and in alphabetical order. These are followed by descriptions of spinithrix forms in which width and thickness are approximately equal, again, in alphabetical order. The section describing spinithrix shape is followed by a section describing modifiers proposed for marginal and then dorsoventral, elaborations. Lastly, apical modifiers are described.

Wherever possible we have adopted terms used previously. For forms to which multiple terms have been applied, we have generally advocated the use of the simplest, most descriptive term. For microthrix forms for which terms do not already exist, we have chosen terms that have their origins in Latin or Greek, which describe the form of the microthrix as closely as possible.

I. Overall shape

A. Spinithrices in which width greatly exceeds thickness

Figs. 2, 4–6

(i) Bifid (shallowly forked) (*bifidus*; L., double)

Figs. 2, 6B, C

These spinithrices possess relatively short prongs, which do not comprise more than half the length of the spinithrix. The component parts, or prongs, can be paral-

lel to one another, converge on one another (e.g., Fig. 6B), or they can diverge from one another (e.g., Fig. 6C). The prongs may be equal or unequal to one another in width; similarly, the prongs may be equal or unequal to one another in length.

(ii) Bifurcate (deeply forked) (*bifurcus*; L., two-pronged)

Figs. 2, 6D

The two prongs of bifurcate spinithrices are relatively long, comprising greater than half the length of the spinithrix. This form appears to be relatively uncommon. To date it has been observed only on the margins of the bothria of certain otobothriid trypanorhynch (e.g., see Palm 2004).

(iii) Cordate (heart-shaped) (*cordatus*; L., heart-shaped)

Figs. 2, 6A

These spinithrices are classically heart-shaped. We propose that this term be used regardless of whether the terminal notch bears a point. At present, this form has been observed only in a small subset of rhinebothriidean taxa (e.g., Healy 2006b).

(iv) Gladiate (sword-shaped) (*gladius*; L., sword)

Figs. 2, 4B–P, 5A–N

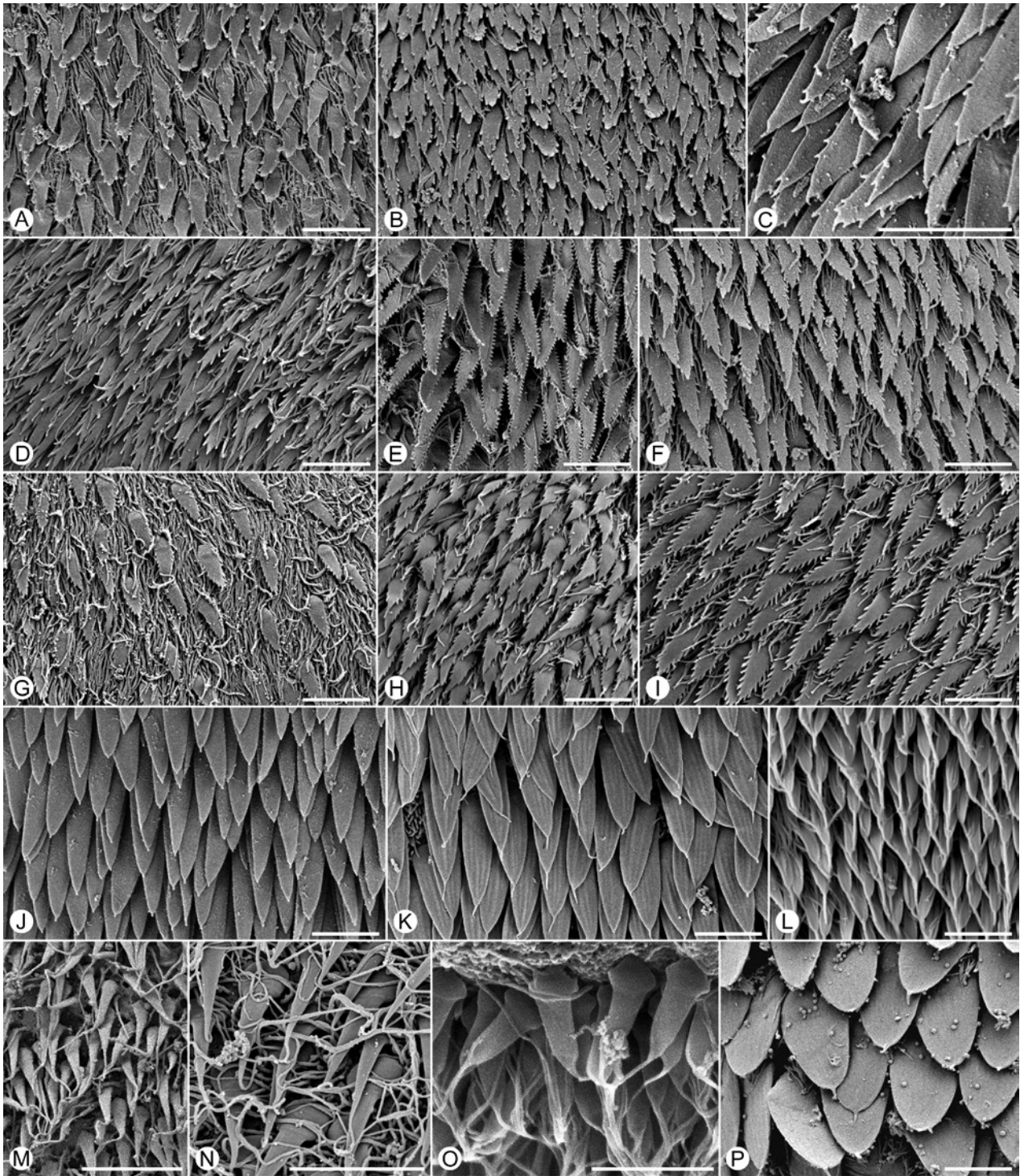
These spinithrices are broadest at their bases, taper to a point, and possess sides that are straight, rather than concave or convex. This is one of the most commonly encountered forms of spinithrix, having been observed in members of a wide spectrum of cestode orders including trypanorhynch, rhinebothriideans, tetraphyllideans, proteocephalideans, and cyclophyllideans. This form varies greatly in size (e.g., compare Figs. 4B–H to Figs. 4N–P) and in the relative proportions of width to length (e.g., compare Figs. 4J and K to Figs. 4N and O). At this point, we have not proposed a formal scheme for the recognition of either of these differences. Such differences could be accommodated by use of the terms small and large or narrow and wide at the beginning of the string of modifiers. However, we suggest that such additional modifiers be used sparingly.

(v) Hamulate (hook-shaped) (*hamulus*; L., hook)

Figs. 2, 4U, 9I

These spinithrices are normally oriented perpendicular to the surface of the tegument so that, unlike most other spinithrices, they appear to be laterally, rather than dorsoventrally, flattened. They are unusual in that they are much thicker than they are wide. These spinithrices possess a relatively broad base and are recurved distally. These are the “hooklike” spinithrices of Palm (2004), who noted that the ultrastructure of these forms differs

Fig. 5. Scanning electron micrographs illustrating marginal and apical modifications of some spinithrix forms in which width greatly exceeds thickness. **A** – Proximal bothridial surface of *Orectolobicestus mukahensis*; **serrate gladiate spinithrices** and **capilliform filitriches**. **B** – Distal bothridial surface of *Orectolobicestus tyleri*; **serrate gladiate spinithrices** and **capilliform filitriches**. **C** – Peduncle of *Paraorygmatobothrium* sp.; **serrate gladiate spinithrices**. **D** – Distal bothridial surface of *Paraorygmatobothrium janinae*; **serrate gladiate spinithrices** and **capilliform filitriches**. **E** – Proximal bothridial surface of *Ruhnkecestus latipi*; **serrate gladiate**



spinitriches and capilliform filitriches. F – Proximal bothridial surface of *Orectolobicestus lorettae*; **serrate gladiate spinitriches and capilliform filitriches. G** – Lateral portion of apical sucker of *Orectolobicestus lorettae*; **serrate gladiate spinitriches and capilliform filitriches. H** – Proximal surface of bothridium of *Paraorygmatobothrium* sp.; **aristate serrate gladiate spinitriches and a few capilliform filitriches. I** – Proximal bothridial surface of *Paraorygmatobothrium janinae*; **serrate gladiate spinitriches and capilliform filitriches. J** – Cephalic peduncle of *Megalonchos sumansinghai*; **aristate gladiate spinitriches. K** – Pedicel of bothridial pair of *Spiniloculus* sp.; **aristate gladiate spinitriches and acicular filitriches. L** – Distal bothridial surface of *Prochristianella* sp.; **aristate gladiate spinitriches and capilliform filitriches. M** – Distal surface of anterior locus of bothridium of new tetraphyllidean genus from *Parascyllum collarae*; **aristate gladiate spinitriches. N** – Distal bothridial surface of *Anthobothrium caseyi*; **aristate gladiate spinitriches and capilliform filitriches. O** – Strobila of *Tetraphyllus lutzi*; **aristate lanceolate spinitriches. P** – Proximal bothridial surface of new tetraphyllidean genus from *Himantura* cf. *gerrardi*; **aristate spathulate spinitriches and capilliform filitriches. Scale bars = 2 μ m.**

substantially from that seen in other spinitriches. For example, they lack a baseplate and the electron-dense portion of the structure appears to be embedded within the outer layer of the tegument, rather than to be associated with an electron-lucent extension of the tegument. In fact, it is possible that these structures are not microtriches at all. Nonetheless, we have included them here, and among the microthrix forms that are greater in diameter in one dimension than in the other, until such time as their structure can be studied in more detail. This form has been observed on the margins of the bothria of trypanorhynch families such as the Tentaculariidae (see Palm 2004); they have also been observed on the cirrus of some cyclophyllideans (e.g., Fig. 9I).

(vi) Lanceolate (narrowing at both ends) (*lanceola*; L., a light spear, lance) Figs. 2, 4S

This term is proposed for spinitriches that taper both at their base and their tip and that are thus widest slightly behind their midpoint. This microthrix form is infrequently encountered, but has been observed on the strobila of the tetrabothriidean *Tetrabothrius lutzi* Parona, 1901 (Ivanov pers. comm.).

(vii) Lineate (resembling a line) (*lineatus*; L., of a line, linear) Figs. 2, 4A

This spinithrix form is conspicuously narrow, possessing sides that are parallel to one another throughout most of their length. However, this spinithrix tapers relatively abruptly to a sharp point. This is a rare form, known to occur in some tentaculariid trypanorhynchs (e.g., Palm 2004).

(viii) Lingulate (shaped like a tongue) (*lingua*; L., tongue) Figs. 2, 4T

This spinithrix form also possesses sides that are generally parallel to one another, but the structure is rounded at its tip. This form has been observed in several different onchobothriid (i.e., tetraphyllidean) genera (e.g., Caira 1992, Caira et al. 2004, 2007a).

(ix) Palmate (having lobes radiating from the margins; resembling an open hand) (*palma*; L., palm of the hand) Figs. 2, 6P–X

Palmate spinitriches possess more than three prongs that originate at different points relative to one another,

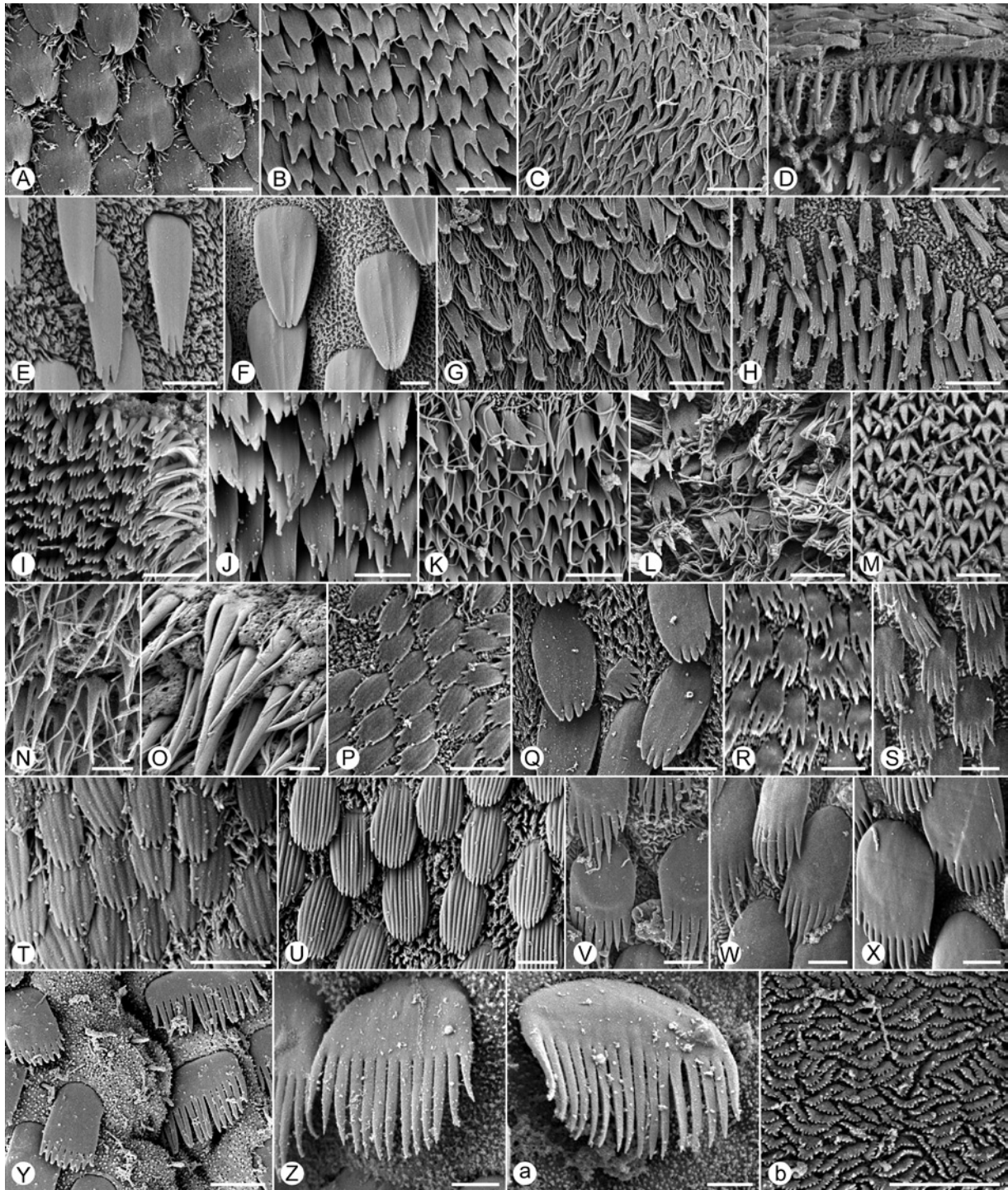
and that also terminate at different points relative to one another. As a consequence, the prongs are often unequal in length. The prongs can be short relative to the length of the spinithrix (e.g., Figs. 6Q, T, U) or long (e.g., Figs. 6R, S, V, W, X). The prongs are generally of equal width. The number of prongs varies from a minimum of 4 (e.g., Fig. 6Q) to at least 11 (Fig. 6X). We recommend that these variations on the basic palmate spinithrix theme, including the number of prongs, be included in the description of the microthrix form. Thus, for example, terms such as quadridigitate, pentadigitate, hexadigitate, may be employed to describe the number of prongs. In some cases, the surface of palmate spinitriches is smooth (e.g., Figs. 6Q, V, X), in other cases, the surface bears superficial ribbing (e.g., Figs. 6T, U). The fact that the ribs are continuous with the prongs in some cases (e.g., Fig. 6T) suggests that palmate spinitriches may be comprised of fused filitriches. However, this will require TEM to resolve. Palmate spinitriches are commonly found on the scolex of trypanorhynchs (e.g., Palm 2004) and diphylloids (e.g., Tyler 2006).

(x) Pectinate (having projections resembling the teeth of a comb) (*pectinatus*; L., comb-like) Figs. 2, 6Y, Z, a, b

Pectinate spinitriches possess more than three prongs arranged parallel to one another. The prongs originate at approximately the same point relative to one another, and also terminate at approximately the same point relative to one another. As a consequence, the prongs are approximately equal in length. To date, variation in the number of prongs ranges from 9 to 16 (e.g., Fig. 6Y). The prongs are generally of equal width. These microtriches have been reported from diphylloids (see Tyler 2006).

It appears that a variation on the pectinate spinithrix theme may occur in some cathetocephalideans. A meaning series of structures, each of which appears to bear numerous short prongs, at least when viewed distally, giving them the appearance of pectinate spinitriches, was observed on the middle region of the base of the scolex of *Cathetocephalus resendezi* Caira, Mega et Ruhnke, 2005 by Caira et al. (2005) (Fig. 6b). These structures differ in orientation from typical pectinate spinitriches in that they appear to be oriented essentially perpendicular, rather than parallel, to the surface. They are very densely arranged and even in a single region can vary substantially in width

Fig. 6. Scanning electron micrographs illustrating some spinithrix forms in which width greatly exceeds thickness. **A** – Proximal bothridial surface and stalks of new genus of rhinebothriidean; **cordate spinitriches** and **capilliform filitriches**. **B** – Apex of scolex just below tentacle of *Hornelliella annandalei*; **bifid spinitriches** and a few **capilliform filitriches**. **C** – Margin of bothrium of *Hornelliella annandalei*; **bifid spinitriches** and **capilliform filitriches**. **D** – Bothrial rim of *Otobothrium mugilis*; **bifurcate and trifid spinitriches**. **E** – Pars vaginalis of *Paroncomegas areiba*; **trifid spinitriches** and **capilliform filitriches**. **F** – Pars vaginalis of *Dolfusiella* sp.; **trifid spinitriches** and **acicular filitriches**. **G** – Proximal bothridial surface *Orectolobicestus randyi*; **trifid spinitriches** and **capilliform filitriches**. **H** – Proximal bothrial surface of *Paragrillotia similis*; **trifid spinitriches** and **capilliform filitriches**. **I** – Distal surface of sucker of *Progynotaenia odhneri*; **trifid spinitriches**. **J** – Pars vaginalis of *Callitetrarhynchus gracilis*; **trifid spinitriches**. **K** – Distal bothrial surface of *Callitetrarhynchus gracilis*; **trifid spinitriches** and **capilliform filitriches**. **L** – Distal bothrial surface of *Lacistorhynchus tenuis*; **trifid spinitriches** and **capilliform filitriches**. **M** – Proximal bothrial surface of *Echinobothrium mexicanum*; **trifid spinitriches**. **N** – Medial distal bothrial surface of *Echinobothrium euterpes*; **trifurcate spinitriches**. **O** – Distal



bothrial surface of *Ditrachybothridium macrocephalum*; **trifurcate spiniriches**. **P** – Proximal bothrial surface of *Lacistorhynchus tenuis*; **palmate spiniriches** and **acicular filitriches**. **Q** – Interbothrial region of eutetrarhynchid; **palmate spiniriches** and **capilliform filitriches**. **R** – Lateral surface of scolex proper of *Echinobothrium rayallemangi*; **palmate spiniriches** and **acicular filitriches**. **S** – Proximal bothrial surface of *Echinobothrium elegans*; **palmate spiniriches** and **acicular filitriches**. **T** – Proximal bothrial surface of *Prochristianella* sp.; **palmate spiniriches** and **capilliform filitriches**. **U** – Pars vaginalis of *Prochristianella* sp.; **palmate spiniriches** and **capilliform filitriches**. **V** – Posterior proximal bothrial surface of *Echinobothrium euterpes*; **palmate spiniriches** and **acicular filitriches**. **W** – Anterior proximal bothrial surface of *Echinobothrium euterpes*; **palmate spiniriches** and **acicular filitriches**. **X** – Proximal bothrial surface of *Echinobothrium rayallemangi*; **palmate spiniriches** and **papilliform filitriches**. **Y** – Proximal bothrial surface of *Echinobothrium hoffmanorum*; **pectinate spiniriches** and **papilliform filitriches**. **Z** – Distal bothrial surface of *Echinobothrium rayallemangi*; **pectinate spiniriches** and **papilliform filitriches**. **a** – Mediodistal bothrial surface of *Echinobothrium hoffmanorum*; **pectinate spiniriches** and **papilliform filitriches**. **b** – Middle region of base of scolex of *Cathetocephalus resendezi*; possible modified pectinate spiniriches. Scale bars: Figs. A–L, P, Q, T, U, Y, b = 2 µm; Figs. M–O, R, S, V–X, Z, a = 1 µm.

and also in the total number of “prongs”. Some appear to bear over 20 of such “prongs”, however, the prong-like structure of these features remains to be confirmed.

(xi) Spathulate (resembling a broad blade) (*spatha*; L., broad blade) Figs. 2, 4I, Q, R

These spinitriches possess a conspicuously broad base and sides that are slightly (e.g., Fig. 4Q) or conspicuously (e.g., Fig. 4R) convex; they taper distally to an inconspicuous point. This form is commonly seen in tetraphyllideans such as *Yorkeria* Southwell, 1927 (e.g., Caira and Tracy 2002).

(xii) Trifid (divided into three relatively short parts) (*trifidus*; L., three-cleft) Figs. 2, 6E–M, 7L

The three prongs of trifid spinitriches are relatively short, comprising half the length of the spinithrix or less. As with bifid spinitriches, the prongs of trifid forms can be parallel to one another (e.g., Figs. 6F, I, L), they can converge upon one another, or they can diverge from one another (e.g., Figs. 6K, M). The prongs can be equal to one another in width (e.g., Figs. 6E, H), or they can be of unequal widths (e.g., Figs. 6J, K). In some cases the prongs are of equal lengths (e.g., Figs. 6I, L); in others they are of unequal lengths (e.g., Figs. 6G, J). Trifid spinitriches have been observed in a diversity of trypanorhynch (e.g., Palm 2004).

(xiii) Trifurcate (divided into three long parts) (*trifurcus*; L., three-forked) Figs. 2, 6N, O

The three prongs of trifurcate spinitriches are long, comprising much of the length of the spinithrix. This form is relatively rare, having been observed to date only in diphyllideans (e.g., Tyler 2006). The slender, elongate prongs of these spinitriches are easily mistaken for capilliform filitriches in instances in which they are closely packed and the basal point of confluence of the prongs is not visible. In some cases, the elongate prongs conspicuously differ in width (e.g., Fig. 6O), in others they are more similar in width (e.g., Fig. 6N).

B. Spinitriches in which width and thickness are approximately equal Figs. 2, 7–9

(xiv) Chelate (pincer-like) (*chela*; L., claw) Figs. 2, 7L

These spinitriches are relatively elongate and round in cross-section; they terminate in a pair of pincer-like digits. They have been likened to the pedicellariae of echinoderms (e.g., Carvajal et al. 1987). To date, this form of spinithrix has been observed, for example, on the margins of the bothria of trypanorhynch of the family Lacistorhynchidae (e.g., Richmond and Caira 1991, Palm 2004).

(xv) Clavate (club-shaped) (*clava*; L., club) Fig. 2

Clavate spinitriches are round in cross-section, but narrower distally than proximally, and they also possess a constriction at about their midlevel. Thus, they resemble bowling pins or clubs in form. This is among the more

unusual spinithrix types. This form may occur in haplobothriideans (e.g., MacKinnon and Burt 1985b, fig. 8). However, to date it is known only from TEM images and it is possible that the shape is an artifact of the plane of sectioning. Nonetheless, this term is appropriate for spinitriches of this form should they be verified to exist.

(xvi) Columnar (column-like in shape) (*columna*; L., pillar) Figs. 2, 7M

These spinitriches are round in cross-section, but possess sides that are parallel to one another throughout most of the length of the spinithrix. However, they generally taper distally to a rounded or, in some instances, relatively pointed end. This form of spinithrix is among those seen, for example, in litobothriideans (e.g., Olson and Caira 2001).

(xvii) Coniform (shaped like a cone) (*conus*; L., cone) Figs. 2, 3M, 7G–K, 9A–D

This form is round in cross-section, possesses straight sides, but, unlike the columnar form, tapers gradually throughout most of its length to a fine point. This form has been observed on the scolices of some trypanorhynch (e.g., Palm 2004), litobothriideans (e.g., Olson and Caira 2001), lecanicephalideans (e.g., Jensen 2005), and on the cirrus of some tetraphyllideans (e.g., Figs. 9C, D) and cyclophyllideans (e.g., Fig. 9B). In the rare cases in which two coniform spinitriches arise from a single base (e.g., Fig. 7K), the term duplicated may be used prior to all other spinithrix modifiers.

(xviii) Costate (bearing longitudinal ridges) (*costatus*; L., ridged, ribbed) Fig. 2

Such spinitriches have ridges that extend parallel to their long axis. The ridges can be confined to the base or extend throughout the length. There may be a single ridge, as for example seen in the tetrathyridium of *Mesocestoides* Vaillant, 1863 by Hess and Guggenheim (1977), or multiple ridges (or “flanges”) may be present, as for example was reported in the cysticeroid of *Ophryocotyle* Friis, 1870 by MacKinnon and Burt (1983). The ridging seen in costate spinitriches is not to be confused with the occurrence of the more delicate surface ribbing seen on some palmate spinitriches (e.g., Figs. 6T, U).

(xix) Cyrillionate (resembling a jug with a narrow neck) (*kyrillion*; G., a jug with a narrow neck) Figs. 2, 7P

These small spinitriches are ovate basally but taper relatively abruptly to a point. The junction between the ovate base and the tapering distal region is relatively abrupt, rather than gradual. These spinitriches appear to be rare. To date they are known from tetraphyllidean genera such as *Nandocestus* Reyda, 2008 (e.g., Reyda 2008).

(xx) Hastate (having the shape of an arrowhead) (*hasta*; L., spear-shaped, arrow-shaped) Figs. 2, 7R–T

These spinitriches are triangular in overall form, and may possess conspicuous basal lobes or shoulders on either side (e.g., Fig. 7T). Hastate spinitriches are perhaps

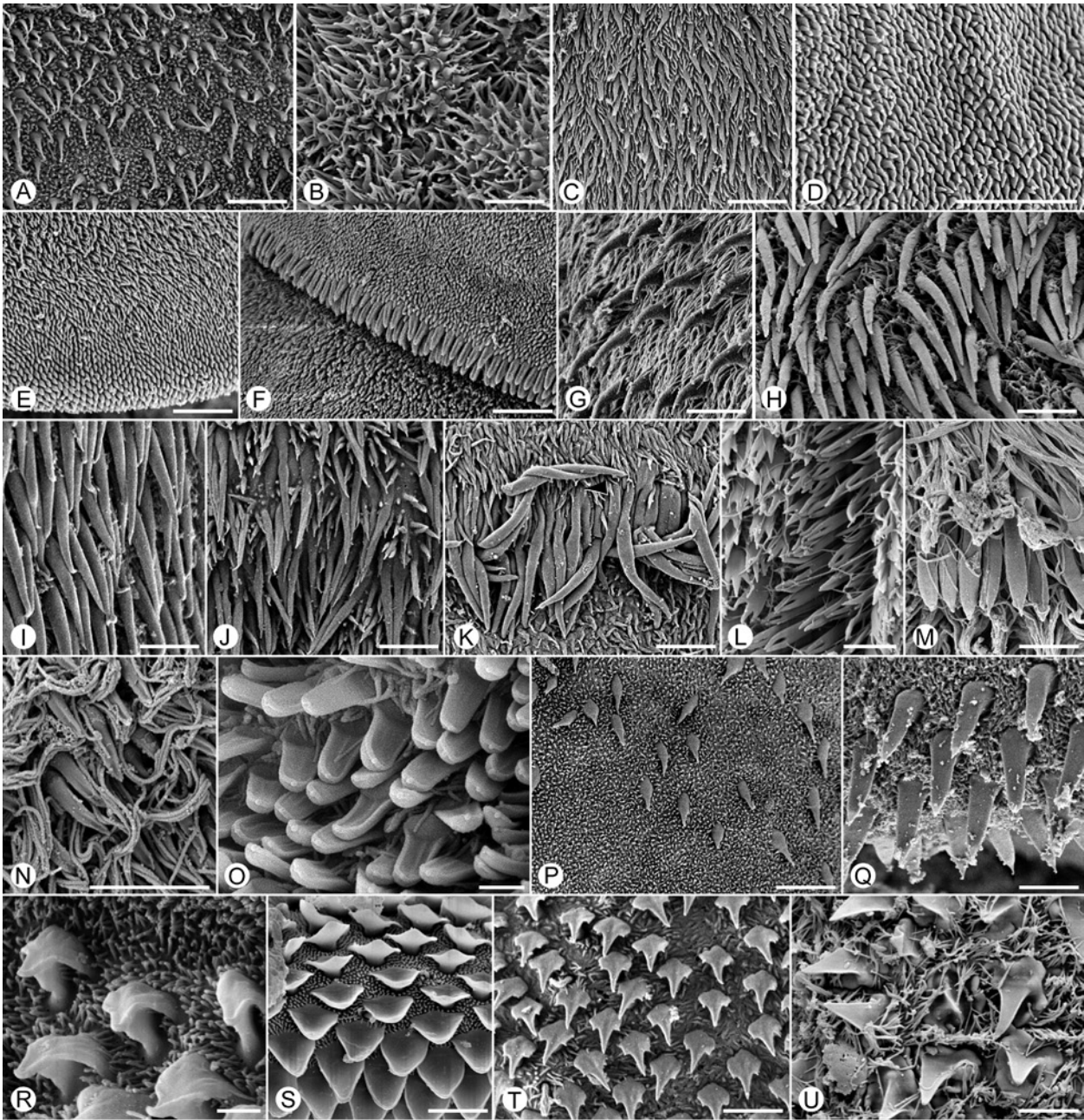


Fig. 7. Scanning electron micrographs illustrating some spinitrich forms in which width and thickness are approximately equal. **A** – Distal bothridial surface of *Scalithrium* sp.; **scolopate spinitriches** and **papilliform filitriches**. **B** – Distal bothridial surface of *Anthocephalum alicae*; **scolopate spinitriches**. **C** – Stalk of *Anthocephalum centrourum*; **scolopate spinitriches** and **acicular filitriches**. **D** – Anterior strobila of *Cephalobothrium* sp.; **scolopate spinitriches**. **E** – Posterior margin of proglottid of *Aberrapex senticosus*; **scolopate spinitriches** (of slightly different sizes). **F** – Posterior margin of proglottid of *Polypocephalus* sp.; **scolopate** and **trullate spinitriches**. **G** – Distal sucker surface of *Cephalobothrium* sp.; **coniform spinitriches** and **acicular filitriches**. **H** – Scolex proper between bothria of *Heteronybelinia estigmene*; **coniform spinitriches** and **capilliform filitriches**. **I** – Apex of scolex of “mushroom” type new litobothriidean; **coniform spinitriches**. **J** – Proglottid of “mushroom” type new litobothriidean; **aristate coniform spinitriches** and **papilliform filitriches**. **K** – Proglottid of “mushroom” type new litobothriidean; **duplicated aristate coniform spinitriches** (arrowhead) and **acicular filitriches**. **L** – Bothrial rim of *Callitetrarhynchus gracilis*; **chelate spinitriches**, **trifid spinitriches** and **capilliform filitriches**. **M** – Posterior margin of first pseudosegment in *Litobothrium daileyi*; **columnar spinitriches** and **capilliform filitriches**. **N** – Rim of sucker of *Lecanicephalum* sp.; **trullate spinitriches** and **capilliform filitriches**. **O** – Distal bothridial surface of *Crossobothrium* sp.; **trullate spinitriches** and **acicular filitriches**. **P** – Proximal bothridial surface near bothridial rim of *Nandocestus guariticus*; **cyrrillionate spinitriches** and **papilliform filitriches**. **Q** – Rim of sucker of *Quadcuspibothrium francisi*; **rostrate spinitriches** and **acicular filitriches**. **R** – Apical modification of scolex proper of new genus of lecanicephalidean; **hastate spinitriches** and **acicular filitriches**. **S** – Sucker margin of *Aberrapex manjajae*; **hastate spinitriches** and **papilliform filitriches**. **T** – Apical modification of scolex proper of *Polypocephalus helmuti*; **hastate spinitriches** and **acicular filitriches**. **U** – Rim of sucker of new lecanicephalidean from *Narcine lingula*; **rostrate spinitriches** and **capilliform filitriches**. Scale bars: Figs. A–N, P, Q, S–U = 2 µm; Figs. O, R = 1 µm.

most easily confused with gladiate spinitriches in instances in which their full thickness (e.g., Fig. 7R) is not visible, or is difficult to observe. This type of spinitrix has been observed on the scolex of cyclophyllidean (Davaineidae) genera such as *Raillietina* Fuhrmann, 1920 and *Cotugnia* Diamare, 1893 (e.g., Bâ et al. 1995) and in a diversity of lecanicephalideans (e.g., Jensen 2005).

(xxi) Rostrate (beak-like) (*rostratus*; L., beaked, curved) Figs. 2, 7Q, U, 9E–G

These spinitriches are abruptly reflexed proximally, which gives them a beak-like appearance. In some instances they bear a complex base (e.g., Figs. 7U, 9F), in others the bases may be simple (e.g., Figs. 7Q, 9E, G). Rostrate spinitriches have been observed in some lecanicephalideans (e.g., Jensen 2001). They have also been observed on the cirrus of some tetraphyllideans (e.g., Reyda 2008).

(xxii) Scolopate (thorn-like) (*skolops*; G., pointed object, thorn) Figs. 2, 7A–F

These are among the smallest spinitrix forms. They possess either straight or slightly convex sides and taper gradually distally. They have been observed in several rhinebothriideans (e.g., Healy 2006a, b) and are relatively common in lecanicephalideans (e.g., Jensen 2005).

(xxiii) Stellate (star-shaped) (*stella*; L., star) Figs. 2, 9J

These spinitriches bear multiple prongs aggregated into a star-like cluster. We believe the structures reported on the cirrus of *Euzetiella tetraphylliformis* de Chambrier, Rego et Vaucher, 1999 by de Chambrier et al. (1999) (Fig. 9J) are of this form. It should be noted that we do not consider spinitriches such as those seen on the cirrus of *Nandocestus* (e.g., Reyda 2008, Fig. 9F) to be stellate; despite the somewhat stellate form of the base, these spinitriches bear only a single structure radiating from this base.

(xxiv) Trullate (shaped like a dipper or scoop) (*trulla*; L., dipper, scoop) Figs. 2, 7F, N, O

These spinitriches bear a concavity on their dorsal surface and thus resemble a dipper or scoop. The concavity may be restricted to a portion of their length (e.g., Fig. 7N), or it may extend throughout their length (e.g., Fig. 7O). They have been observed to date in bothriocephalideans such as *Paraechinophallus* Protasova, 1979 (e.g., the “tusk-like” spinitriches described by Levron et al. 2008a), in some lecanicephalideans (e.g., Jensen 2005), and in tetraphyllideans such as *Crossobothrium* (Ivanov pers. comm.).

(xxv) Uncinate (hook-shaped) (*uncinatus*; L., hooked) Figs. 2, 9H

Unlike hamulate spinitriches, these hook-shaped spinitriches are not laterally flattened, rather they have a substantial width (and also thickness) to them. These spinitriches usually conspicuously curve posteriorly. They

have been observed on the cirrus of some tetraphyllideans (e.g., Fig. 9H) (Caira unpubl.).

II. Marginal and/or dorsoventral modifications

As noted above, in the terminology described here, marginal and/or dorsoventral modifications are considered independently of spinitrix shape. This is because it appears possible for spinitriches of a variety of different forms to exhibit apical and marginal and/or dorsoventral modifications. Thus, while many spinitriches are entirely smooth, a number of spinitrix forms bearing projections have also been observed. Such projections can be restricted to the lateral margins, or to the dorsal surface, or they can be found on all surfaces of the spinitrix. They can occur throughout the length of the spinitrix, or they can be restricted to only a portion of the length of the spinitrix. The projections are narrow, but can vary somewhat in length.

We have attempted to simplify the terminology used to describe marginal and dorsoventral spinitrix projections by recognising only two nominal categories of such modifications: serrate and gongylate. In the former case, the projections are restricted to the margins of the spinitrix; in the latter case they are more extensively distributed, occurring somewhere on the dorsal and/or ventral surfaces. We believe that this scheme will accommodate at least all of the variation seen to date, and hopefully is sufficiently flexible to also accommodate at least some of the potential variation not yet observed.

Serrate (with forward-projecting teeth) (*serra*; L., saw) Figs. 2, 3L, 5A–I

Serrate spinitriches are those that bear marginal projections. In all cases these projections are forward pointing; they can vary in length; long projections are seen in some taxa (e.g., Figs. 5D, I), and shorter projections exist in others (e.g., Figs. 5C, E). The projections can be evenly spaced along the margins (e.g., Figs. 5E, F, H, I), or they can be more irregularly spaced (e.g., Figs. 5A–C). In some cases, the marginal projections occur along the entire length (e.g., Figs. 5H, I); in other cases they appear to be restricted to a portion of the distal half of the spinitrix (e.g., Fig. 5C). In rare instances, spinitriches bearing what appear to be both a dorsal and ventral band of marginal projections have been seen (e.g., Fig. 3L). We recommend that such variation in length and spacing of the projections be noted. However, we have not developed specific terminology to accommodate such variation. Spinitriches in which all of the projections are restricted to the distal lateral margins should be considered palmate, rather than serrate.

Serrate spinitriches have been reported from tetraphyllidean cestodes, most commonly from the tetraphyllidean genera *Paraorygmatobothrium* (e.g., Ruhnke and Carpenter 2008) and *Orectolobicestus* (e.g., Ruhnke et al.

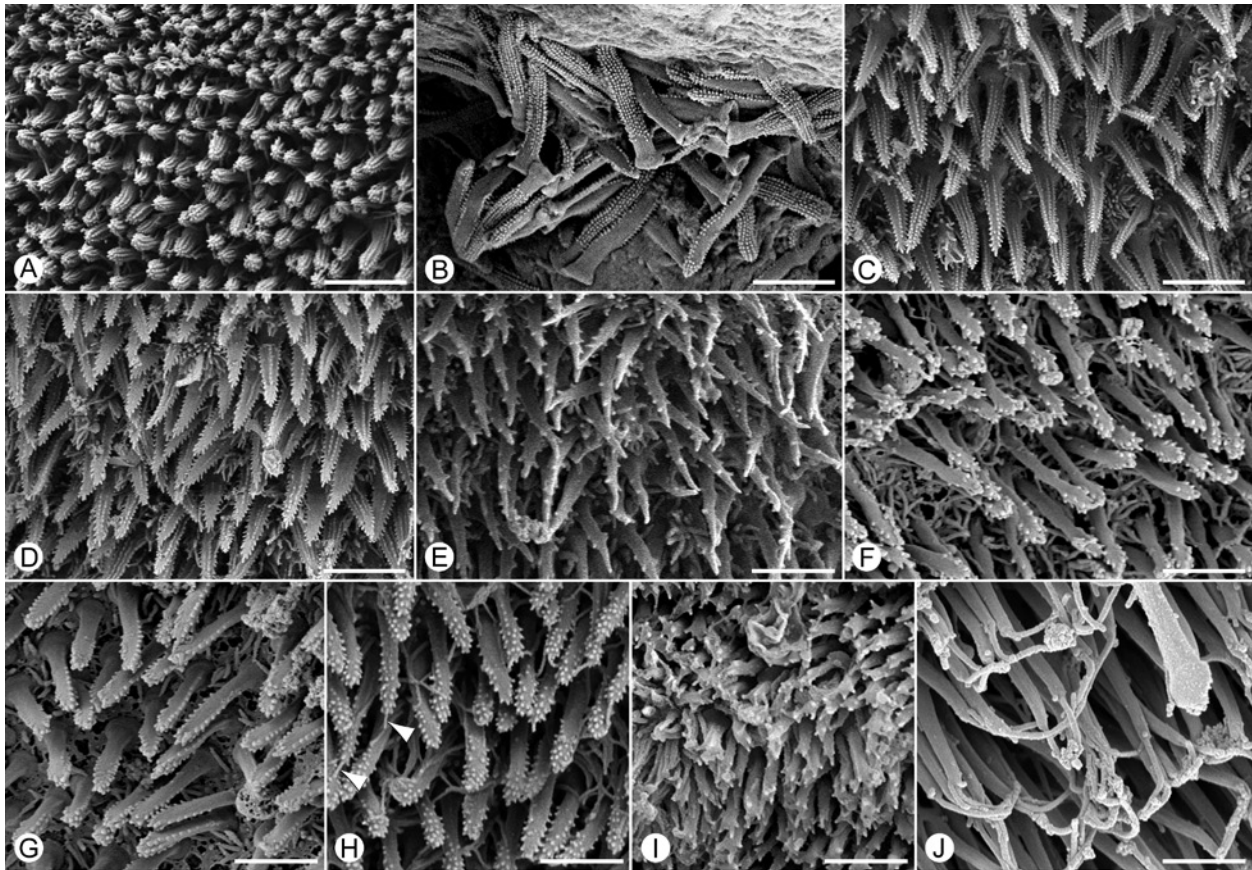


Fig. 8. Scanning electron micrographs illustrating dorsoventral modifications of some spinitrich forms in which width and thickness are approximately equal. **A** – Distal bothridial surface of *Phyllobothrium squali*; **gongylate columnar spinitriches** and **capillate filitriches**. **B** – Distal bothridial surface of *Pithophorus* sp.; **gongylate columnar spinitriches** (projections restricted to distal surface). **C** – Distal surface of *Paraorygmatobothrium* sp.; **gongylate coniform spinitriches** and **acicular filitriches**. **D** – Distal surface of *Paraorygmatobothrium* sp.; **gongylate coniform spinitriches** and **acicular filitriches**. **E** – Distal bothridial surface of *Anthocephalum* sp.; **gongylate coniform spinitriches** and **acicular filitriches**. **F** – Distal bothridial surface of *Orectolobicestus kelleyae*; **gongylate columnar spinitriches** (projections restricted to distal tips) and **capilliform filitriches**. **G** – Distal surface of marginal loculus on bothridium of *Orectolobicestus mukahensis*; **gongylate columnar spinitriches** and **acicular filitriches**. **H** – Distal bothridial surface of *Orectolobicestus lorettae*; mixture of **gongylate columnar spinitriches** and **aristate gongylate columnar spinitriches** (white arrowheads) and **capilliform filitriches**. **I** – Distal bothridial surface of *Clistobothrium montaukensis*; **gongylate columnar spinitriches** (projections restricted to distal tips; projections somewhat longer than typically seen). **J** – Distal surface of bothridial apical sucker of *Marsupiobothrium* sp.; **columnar spinitriches** with three terminal projections of unequal length. Scale bars: Figs. A–D = 2 µm; Figs. E–J = 1 µm.

2006a). They have also been observed in trypanorhynch genera such as *Grillotia* Guiart, 1927 (e.g., Palm 2004).

Gongylate (bearing multiple small projections) (*gongylos*; G., ball, round, spherical) Figs. 2, 8A–H

Gongylate spinitriches bear at least some projections on their dorsal and/or ventral surfaces. The projections can be small and ball-like (e.g., Fig. 8B), or more elongate, approaching the length of those seen on serrate spinitriches (e.g., Figs. 8C, D). Substantial variation is seen in the distribution of the projections. In many cases, the projections occur on both the dorsal and ventral surfaces (e.g., Figs. 8A, C, D); in rarer cases they are restricted to one side, normally the dorsal surface (e.g., Fig. 8B). The projections can occur throughout the length (e.g., Fig.

8C) or they can be restricted to, or at least concentrated at, the distal tip (e.g., Fig. 8F). The projections are often arranged in regular columns (Figs. 8A, C, D). However, they can also be arranged relatively irregularly (e.g., Fig. 8F), and in a number of cases they are concentrated on the margins (e.g., Figs. 8E, G). It was the column-like arrangement of projections that led authors to refer to this form as “ear-of-corn” (Whittaker and Carvajal 1980), and “maiziform” (e.g., Caira et al. 1999). We recommend that such variation in the arrangement of projections on gongylate spinitriches be noted, but again, we have refrained from developing a more specific terminology to describe this variation at this time.

Gongylate spinitriches have been observed in tetraphyllidean cestodes, most commonly those of the gen-

era *Paraorygmatobothrium* (e.g., Ruhnke and Carpenter 2008), *Orygmatobothrium* (e.g., Ivanov 2008), and *Orectolobicestus* (e.g., Ruhnke et al. 2006a).

It appears that several variations on the gongylate spinithrix theme may occur in at least some tetraphyllidean taxa. For example, *Clistobothrium* Dailey et Vogelbein, 1990 appears to possess spinitriches that bear a ring of projections around the margin of their distal surface (Fig. 8I). However, little is known of this form and available images suggest that these structures might actually represent a fusion of multiple capilliform filitriches (Caira, pers. obs.). In addition, spinitriches bearing multiple terminal projections of markedly unequal length (e.g., Fig. 8J) have been observed in other tetraphyllideans. Again, at present it is not clear how this form should be interpreted. Additional data are required before it can be fully categorised.

III. Apical modifications

Aristate (having a bristle-like tip) (*arista*; L., bristle)
Figs. 5J–O

Aristate spinitriches bear a bristle-like tip. Some variation in the length of this projection occurs. In some species it is relatively short (e.g., Figs. 5J, O), in others it is relatively long (e.g., Figs. 5K, L), in yet others it is conspicuously long, sometimes approaching the length of the spinithrix proper (e.g., Figs. 5M, N). We recommend that apical projections be noted when observed. It appears that a diversity of spinithrix forms can bear an apical projection. For example, aristate gladiate spinitriches (e.g., Figs. 5J, K, M, N), aristate lingulate spinitriches (Fig. 5L), aristate spatulate spinitriches (e.g., Fig. 5P) and aristate lanceolate spinitriches (e.g., Fig. 5O) are known to exist. Aristate coniform spinitriches have also been observed (e.g., Fig. 7J).

Aristate modifications of spinitriches have been observed, for example, in tetraphyllidean genera such as *Pedibothrium* Linton, 1908 (e.g., Caira 1992, Caira et al. 2004), *Yorkeria* (e.g., Caira and Tracy 2002), *Anthobothrium* van Beneden, 1850 (e.g., Ruhnke and Caira 2009), and also in litobothriideans (e.g., Olson and Caira 2001), and tetrabothriideans (Fig. 5O).

SUMMARY OF TERMINOLOGY

Fig. 2 was designed to summarise, and thereby facilitate application of, the terms proposed above for filitriches and spinitriches. For the sake of consistency, we recommend that the proposed modifiers precede the term spinithrix or filithrix in the sequence shown in Fig. 2. Schematic representations are also provided to illustrate some of the combinations of terms that can, for example, be applied to a particular length (e.g., acicular) of filithrix, and to two particular shapes of spinitriches (i.e., gladiate and columnar).

Filitriches (≤ 200 nm in basal width) Fig. 2

Given that variation in filitriches generally involves only length, most filitriches will require only one modifier in a sequence, i.e., the length modifier. Thus, collectively, the terms papilliform filithrix, acicular filithrix, and capilliform filithrix capture most of the diversity seen in filitriches. Only a single length modifier should be applied to any particular filithrix. In the few instances in which two of these structures arise from a single base, an additional modifier is required. In the case of such duplications, the additional modifier “duplicated” should precede the length modifier. Given the rarity of the duplicated condition, the use of a specific term for the single condition is not advocated.

Spinitriches (>200 nm in basal width) Fig. 2

Variation seen in spinitriches requires a more complex terminology. As many as three modifiers in sequence may be required to fully describe some spinithrix morphologies. Once again, for the sake of consistency, we recommend that these modifiers precede the term spinithrix in the specific sequence shown from left to right in Fig. 2. The shape modifier immediately precedes the term spinithrix. At this point we recognise 25 different spinithrix forms; 13 of these describe variations in spinitriches that are wider than they are thick, and 12 of these describe variations in spinitriches that are approximately as wide as they are thick. Only a single shape modifier should be applied to any particular spinithrix; descriptions of all spinitriches should be accompanied by one of these shape modifiers. The marginal and/or dorsoventral modifier precedes the shape modifier in sequence, but only in the cases of spinitriches that exhibit such modifications. To date, only two options for the marginal and/or dorsoventral modifier have been articulated (i.e., serrate and gongylate). In the absence of a marginal and/or dorsoventral modifier, a spinithrix should be assumed to lack such projections (i.e., the use of a specific term for spinitriches that lack such projections is not advocated). The apical modifier precedes the marginal and/or dorsoventral modifier (if present) in sequence, but only in the cases of spinitriches that exhibit an apical modification. To date the only apical modification observed is the presence of a bristle-like (i.e., aristate) tip. Once again, in the absence of the apical modifier, a spinithrix is assumed to lack an apical modification (i.e., the use of a specific term for spinitriches lacking an aristate tip is not advocated).

FUTURE CONSIDERATIONS

Given the relatively broad suite of taxa that has been examined for microthrix variation, a pattern has begun to emerge indicating likely avenues to pursue for the discovery of additional microthrix variation. With respect to filitriches, acicular and capilliform filitriches appear to be

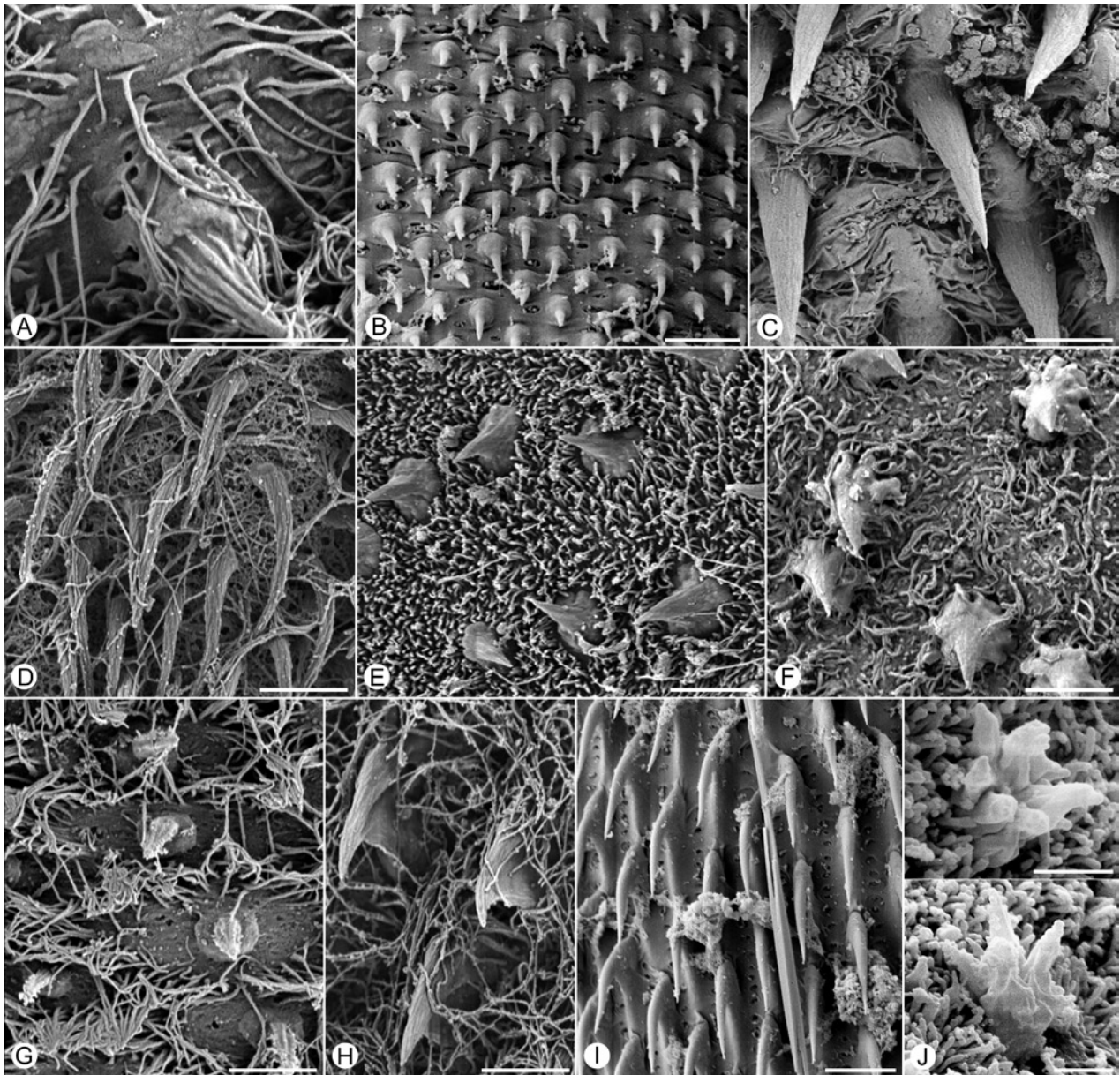


Fig. 9. Scanning electron micrographs illustrating cirrus microtriches. **A** – Cirrus of *Rhinebothrium* sp.; **coniform spinithrix** and **capilliform filitriches** with unusual bases. **B** – Distal region of cirrus of *Progynotaenia odhneri*; **coniform spinithrix**. **C** – Cirrus of *Rhinebothrium* sp.; **coniform spinithrix** and **capilliform filitriches**. **D** – Cirrus of new genus of tetraphyllidean from *Pristis clavata*; **coniform spinithrix** and **capilliform filitriches**. **E** – Cirrus of new genus of tetraphyllidean from *Pristis clavata*; **rostrate spinithrix** and **capilliform filitriches**. **F** – Cirrus of *Nandocestus guariticus*; **rostrate spinithrix** (with **stellate bases**) and **capilliform filitriches**. **G** – Cirrus of *Rhinebothrium copianullum*; **rostrate spinithrix** and **capilliform filitriches**. **H** – Cirrus of new genus of tetraphyllidean from *Pristis clavata*; **uncinate spinithrix** and **capilliform filitriches**. **I** – Proximal region of cirrus of *Progynotaenia odhneri*; **hamulate spinithrix**. **J** – Cirrus of *Euzetiella tetraphylliformis*; **stellate spinithrix** and **acicular filitriches** (shown two slightly different views). Scale bars: Figs. A–H, J = 2 µm; Fig. I = 4 µm.

widely distributed, and perhaps even ubiquitous, among the tapeworm orders. Papilliform filitriches appear to be more restricted taxonomically. We predict that little additional variation will be found in filitrix form.

The situation with spinithrix is likely to be quite different. Gladiate and coniform spinithrix, of a variety of widths and sizes, are by far the most commonly seen

spinithrix shapes, each having been observed in members of most orders of tapeworms. This is not the case for the other spinithrix shapes. In fact, most of the other 23 spinithrix shapes, and also spinithrix with marginal and/or dorsoventral and apical modifications, have been reported solely from the elasmobranch-parasitizing orders Trypanorhyncha, Diphyllidea, Lecanicephalea,

Tetraphyllidea, and Rhinebothriidea. Since these groups are in need of further study, they are likely to continue to be productive avenues of spinithrix investigation. As data on these taxa continue to be compiled, it seems likely that spinithrix forms may be found to represent useful synapomorphies for subsets of these taxa. In addition, preliminary data available on cyclophyllidean families other than the Taeniidae (e.g., the Hymenolepididae, Anoplocephalidae, Davaineidae, etc.) have revealed a diversity of interesting spinithrix forms (e.g., Bâ et al. 1995). Furthermore, the fact that at least some of the rostellar elements of these and other taxa, which have up to now been interpreted as hooks, hooklets, or spines, may be determined to be large microtriches (e.g., Mount 1970, Thompson et al. 1980, Biserova 1991, Stoitsova et al. 2001), provides a number of intriguing avenues for investigation. This is likely also true for at least some of the structures associated with the rostellum of some proteocephalideans (Scholz et al. 1999).

Examination of the surface of the cirrus and lining of the vagina of a diversity of tapeworms suggests that these organs are also worthy of further attention, particularly in the cestode orders in which they have not been explored in much detail to date. We have presented exemplar images of microtriches from cirrus surfaces (Fig. 9) separately from images of microtriches found on the various surfaces of the scolex and strobila (Figs. 3–8) in an attempt to illustrate some of the trends that appear to be emerging with respect to cirrus microtriches. For example, unlike most other regions of the body, it is not uncommon to find cirri bearing spinithrices, but lacking filitriches (e.g., Figs. 9B, I). There appears to be much less variation in the form of cirrus microtriches than seen among microtriches elsewhere on the body; those of the cirrus tend to be coniform, uncinata, or rostrate. However, the extent to which these observations can be generalised across cestode taxa requires substantial additional work, as do generalisations regarding the form of vaginal microtriches. We predict that additional work on the surfaces of these reproductive structures across a diversity of taxa will yield additional forms. It is also likely that progress will be greatly facilitated by the use of a combination of SEM and TEM methods. For example, the recent work of Poddubnaya and Mackiewicz (2009) provided some interesting interpretations of the surface features on the cirri of two species of echinophallids (Bothriocephalidea).

Although several studies have addressed the processes by which microtriches are formed, our understanding of the development of these structures remains far from complete. In general, the tegument of cestode larvae (i.e., the hexacanth sensu Conn and Świderski 2008) bears microvilli, while that of metacestodes (sensu Chervy 2002) and adults bears microtriches (see Conn 2004, Conn and Świderski 2008). However, several scenarios have been described with respect to the actual formation of microtriches. The primary distinction among scenarios appears

to be whether microtriches are formed *de novo*, or via the conversion of microvilli by the addition of electron-dense material to form the cap (e.g., Hulínská 1980, MacKinnon and Burt 1984). Two scenarios of formation *de novo* have been described. Either the microthrix forms below the plasmalemma and is erected (e.g., Timofeev and Kuperman 1972, Lumsden et al. 1974, Hess 1980), or electron-dense material is added beneath the plasmalemma followed by formation of the base (e.g., Richards and Arme 1984). In some cases, both of these modes of *de novo* formation have been reported in the same taxon (e.g., Rogan and Richards 1987). There even exist reports of both the transformation of microvilli into microtriches and the *de novo* formation of microtriches in the same stage of the same species (e.g., Davydov et al. 1995). It remains to be determined if the differences observed can be attributed to differences among taxa, developmental stages, or sites within a species. However, it is interesting that different processes have been reported within the same developmental stage of the same species (e.g., Ubelaker 1980, Richards and Arme 1984). Clearly, much work remains to be done in this area. Furthermore, Biserova (1991) actually considered the hooks of the rostellum and peduncle of diphyllideans to be homologous with the microtriches she recognised as “polymicrotriches”.

Finally, while the potential functions of microtriches have been discussed on numerous occasions (e.g., Threadgold 1962, Rothman 1963, Morseth, 1966, McVicar 1972, Lumsden, 1975b, Lumsden and Murphy 1980, Thompson et al. 1980, Lumsden and Hildreth 1983, Coil 1991, Hayunga 1991), in fact, much remains to be learned of the roles microtriches *actually* play in the lives of cestodes. Among the functions attributed to microtriches are: absorption of nutrients, amplification of the absorptive surface area, attachment to the surface of the host intestinal tract either to aid in movement, or to prevent expulsion, agitation of their microhabitat, abrasion of the mucosal surface so as to increase the concentration of nutrients adjacent to the worm, warding off of host cells, and maintaining a barrier between the tegument and the mucosal surface. However, at least some of these roles have never been definitively documented. Evidence also exists that microtriches play an integral role in the formation of certain “hard” structures in cestodes. For example, Mount (1970) provided convincing evidence that the rostellar hooks of *Taenia crassiceps* (Zeder, 1800) originate through the enlargement of spinithrices. However, the processes by which hooks are formed in most other cestode groups remain completely unknown. Also, given the diversity of cestode epithelial structures described to date (see Jones 1998), it would be interesting to know if microtriches play a role in the function of any of these other structures.

All data to date suggest that microtriches are restricted to members of the class Cestoda. Reports of these structures from species belonging to other invertebrate taxa appear to be unjustified. For example, the acanthocephalan

surface features identified as microtriches by Amin et al. (2009) lack the key features of microtriches as articulated here and thus should be discounted as erroneous reports.

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