Five types of colloblast in a cydippid ctenophore, *Minictena luteola* Carré and Carré: an ultrastructural study and cytological interpretation

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SUMMARY

Minictena luteola Carré and Carré is a recently described, small mediterranean ctenophore, with five types of colloblast. We have examined the morphology of the colloblasts at different stages of differentiation by electron microscopy. The five types differ in size and structure at all stages of differentiation.

This is the first report of colloblast polymorphism in ctenophores. Two of the types found in *M. luteola* differ significantly from the generally accepted structure of colloblasts, in particular by the absence of refractive vesicles. Examination of the structure of the five types of colloblast during differentiation has given us a better idea of the nature and organization of the axial filament and the origin of the spheroidal body and its relationship with the nucleus. Our observations lead us to question the axonemal nature of the spiral filament.

1. INTRODUCTION

All ctenophores, except those in the families Beroidae and Hæckeliidae, have two tentacles armed with colloblasts. These are sticky cells whose function is still not well understood. Colloblasts from different species have been described by light microscopy (Chun 1880; Schneider 1902; Komai 1922; Weill 1935) and electron microscopy (Hovasse & de Puytorac 1962; Bargmann *et al.* 1972; Storch & Lehnert-Moritz 1974; Benwitz 1978; Franc 1978; Mackie *et al.* 1988; Emson 1991). Differences have been noted in the size and the number of turns in the spiral filament (Franc 1978), although it has been generally assumed that only one type of colloblast exists in each ctenophore species.

In general organization, colloblasts have an hemispherical head (collosphere) and a conical stalk (collopod) embedded in the underlying muscle. The head is covered by a layer of external granules (refractive vesicles) and contains internal granules connected by fine rays (radii) to a spheroidal body lying beside the nucleus. Previous authors have described in the stalk separate axial and spiral filaments. Komai (1922) and later authors, with the exception of Bargmann *et al.* (1972), interpreted the axial filament as being a strand of cytoplasm with an elongated nucleus, extending the entire length of the collopod. The spiral filament was thought to be a modified intracellular axoneme (Storch & Lehnert-Moritz 1974; Benwitz 1978) that emerges from the spheroidal body, spirals with one or two turns and finishes by a root, often striated (Benwitz 1978; Franc 1978) comparable with a flagellar rootlet.

We suggested from previous *in vivo* observations, that in *Minictena luteola*, a small (2 mm long) ctenophore, there is polymorphism of colloblasts (Carré & Carré 1993). The colloblasts, found in the tentilla of the tentacle, vary both in size and in morphology. Here we confirm this polymorphism by electron microscopy. Each tentilla carries five types of colloblasts. By studying them at all the main phases of differentiation, we have been able to question the axonemal nature of the spiral filament and describe the origin of the spheroidal body, considered by Hovasse & de Puytorac (1962) as an extrusion of the nucleus.

2. MATERIALS AND METHODS

Specimens of *M. luteola* were collected in October and November in the surface waters (0–50 m) of the Bay of Villefranche-sur-mer (Ligurian sea, Mediterranean) with a 50 µm mesh net. *In vivo* observations were made with a Nachet 300 interference contrast microscope. Specimens for electron microscopy were fixed according to Eisenman & Alfert (1982) and embedded in Spurr resin. Ultrathin sections were observed on a Hitachi HM 600 microscope.

3. RESULTS

Tentacles of *M. luteola* have branching tentilla. Each tentilla has a muscular axis covered by epithelial cells,

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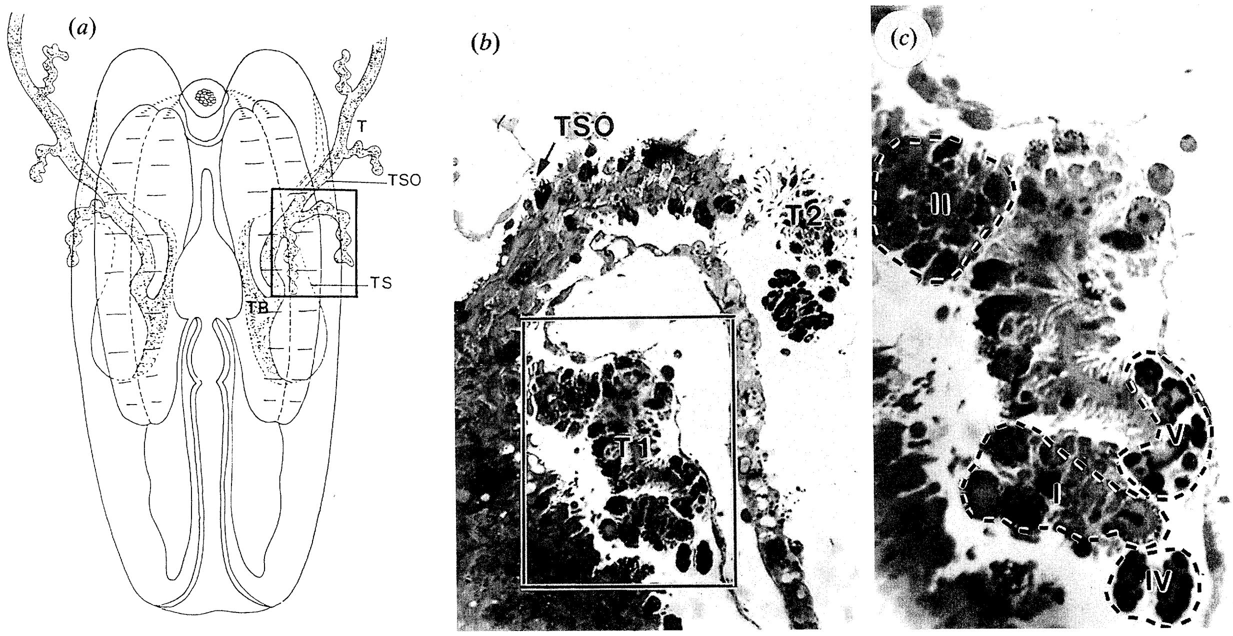

Figure 1. (*a*) Schematic diagram of *Minictena luteola* (tentacular plane) (1.5 mm). Tentacle (T) emerges from the tentacle sheath (TS); (TB, tentacle base; TSO, tentacle sheath opening). (*b*) Semi-thin section across two tentilla (T1 and T2) of the tentacle (T). (*c*) Tentilla T1 detail, colloblasts of one type are grouped together.

sensory cells (both hoplocytes and vibroreceptors) and colloblasts. We have limited our description to the five types of colloblasts present in the tentilla at their main stages of differentiation. In each tentilla, colloblasts of one type are grouped together (figure 1). The biggest ones (type IV and V) are always located at the end of the tentilla.

(*a*) *Type I colloblasts* (figures 2 and 3)

Type I colloblasts are about 14 µm long overall. The collosphere is nearly spherical and 5 µm in diameter, 6 µm including the external granules (figures 2I and 3*a*). Internal granules (0.7 µm in diameter) form a regular layer at the collosphere periphery. Each granule is linked to the spheroidal body by a straight, non-twisted radial structure or radius, 0.18 µm in diameter. Each radius is composed of about 20 filamentous sub-units, which are usually arranged as two concentric hollow cylinders (figure 3*b*,*c*). In the region where a radius is fixed to the granule, it is enlarged and shows transverse striation (figure 3*b*). Beneath the internal granules lie small (60 nm) electron-dense, membrane-free granules (figure 3*b*). Between the radii, the cytoplasm is dense, containing packed mitochondria, saccule sheaths of endoplasmic reticulum and ribosomes.

The spheroidal body, located at the centre of the collosphere where the radii converge, is hemispherical, about 1 µm in diameter (figure 3*a*,*b*). It is electron-dense, with an even denser zone around the periphery where the radii are in contact. In fully differentiated colloblasts, the spheroidal body is located near the tip of the nucleus, but without any link to it (figure 3*h*).

The spheroidal body forms the end of a rectilinear filament running up the collopod axis (figure 3*g*). This filament contains fine granulation and is slightly less dense than the spheroidal body. About three-fifths of the way down the colloblast, it turns in one or two oblique spirals around the nucleus and then runs straight again to the base (figure 3*a*,*g*). It ends with a very electron-dense, non-striated conical root, around which short fibres project towards the plasma membrane (figure 3*a*,*f*).

Transverse and longitudinal serial sections confirmed that a single filament starts beneath the spheroidal body and continues first as a straight axial filament, then with one or two spiral turns and finally as a straight axial filament again. This filament shows the same structure all along its length, with a dense, homogenous central region, 0.5 µm in diameter, surrounded by 10 or 11 microtubules (MT) (depending on the cell) and a complex enveloping membrane (figure 3*d*,*e*). Transverse sections reveal that this envelope folds to form a groove opened to the cytoplasm with several folds at each edge, parallel to the filament axis. This forms during colloblast differentiation from two unconnected folds in the plasma membrane (figure 9). The envelope runs from just beneath the spheroidal body to just above the root (figure 3*b*,*f*).

(*b*) *Type II colloblasts* (figures 2 and 4)

These are very similar to type I. They are distinguished by their size (collosphere diameter of 4 µm) and by their radii, which are often wavy rather than straight (figure 4*a*,*b*). Since colloblasts of intermediate size between type I and II are not found, they probably represent two discrete categories.

(*c*) *Type III colloblasts* (figures 2 and 5)

These are small colloblasts not distinguishable by

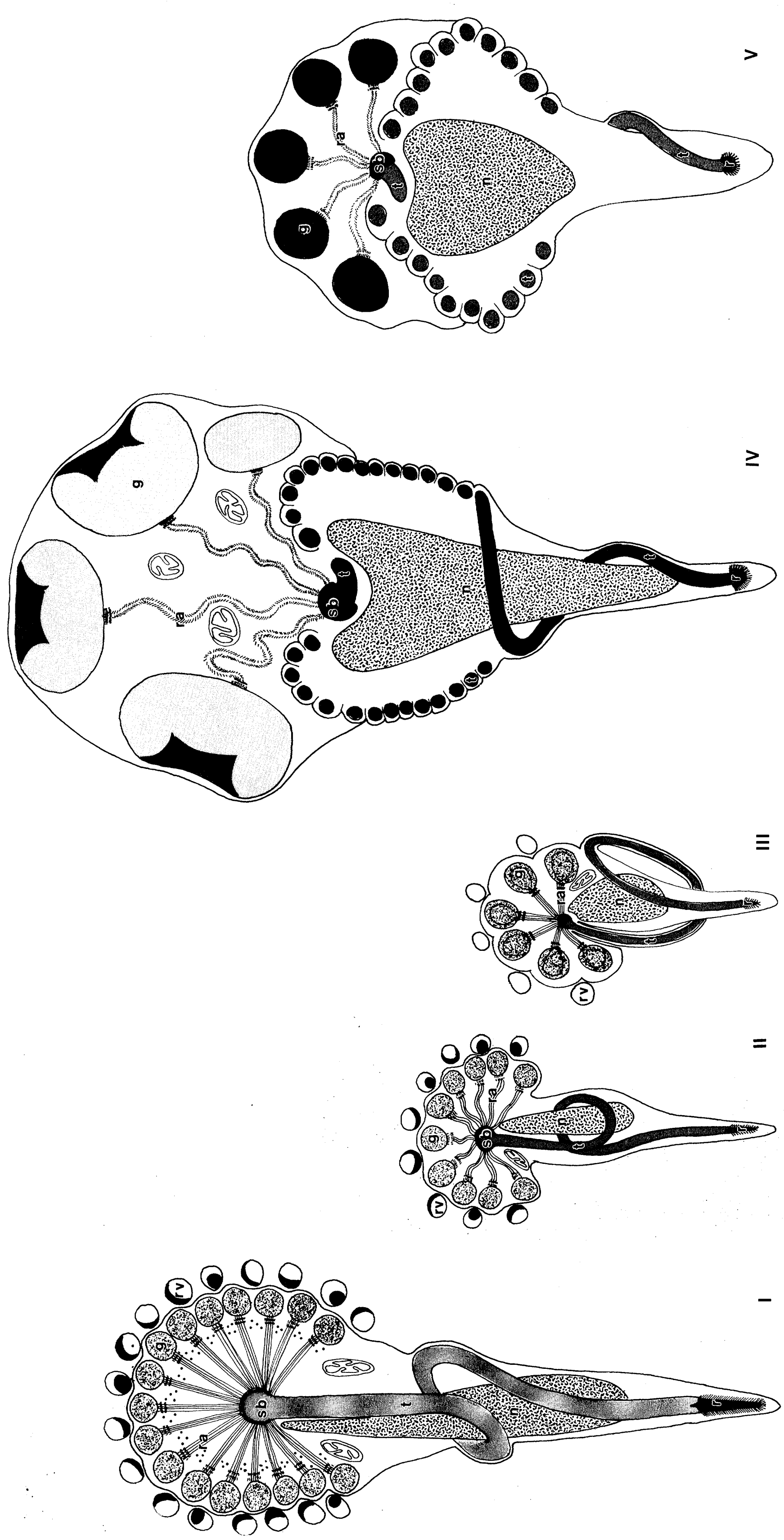

Figure 2. Types I to V colloblasts drawn to scale demonstrating their main features. The membrane grooves surrounding the filament and longitudinal MT are not shown. In types IV and V, the upper part of the filament is shown in section.

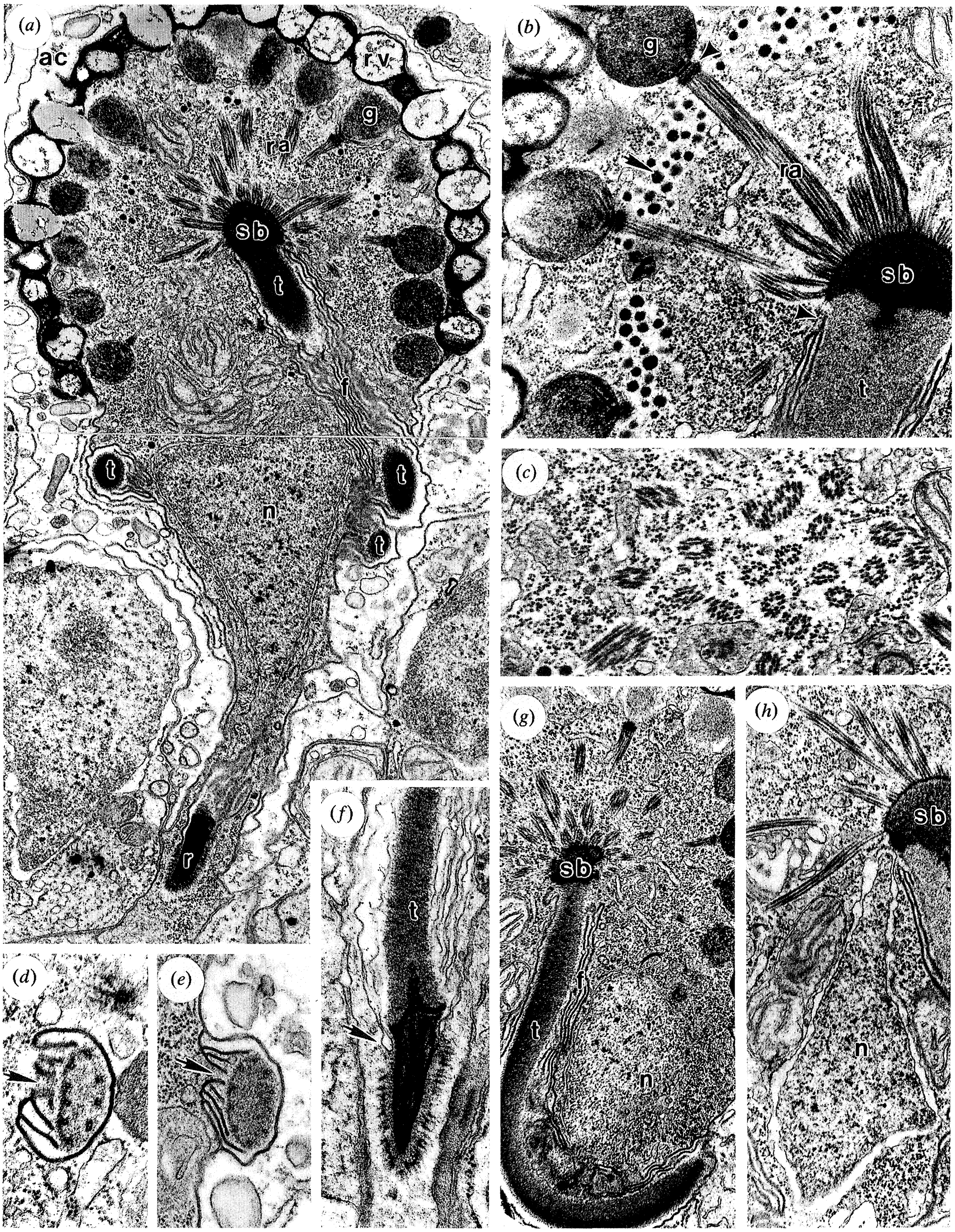

Figure 3. Type I colloblasts. (*a*) Longitudinal section at the end of differentiation; accessory cell (ac) is still present. The section passes through the beginning of the filament (t) beneath the spheroidal body (sb) and by the longitudinal folds (t) of the membranal groove surrounding the filament. Note the spirals cut transversally (t). × 13 500. (*b*) Collosphere detail: radii (ra) linking internal granules (g) to the spheroidal body (sb) are straight; they join the granules at a differentiated zone (upper arrow). Note the presence of opaque granulations (lower arrow). The membrane groove surrounding the filament starts beneath the spheroidal body. × 23 500. (*c*) Transverse section of radii. They are composed of two concentric filamentous cylinders. × 29 500. (*d*) Transverse section in the straight part of the filament. It is surrounded by nine MT. The enveloping membrane groove communicates with the cytoplasm (arrow). × 34 500. (*e*) Transverse section of the spiral part of a filament surrounded by ten MT. Communication with the colloblast cytoplasm (arrow) is maintained. × 24 500. (*f*) Root at the end of the filament. Note the absence of transverse striations and the end of membrane groove above the root (arrow). × 29 500. (*g*) Longitudinal section showing continuity between the axial straight portion and the spiral portion of the filament. × 12 000. (*h*) Spheroidal body–nucleus junction. The apex of the nucleus (n) is in contact with the spheroidal body but the nuclear membrane is intact. × 16 500.

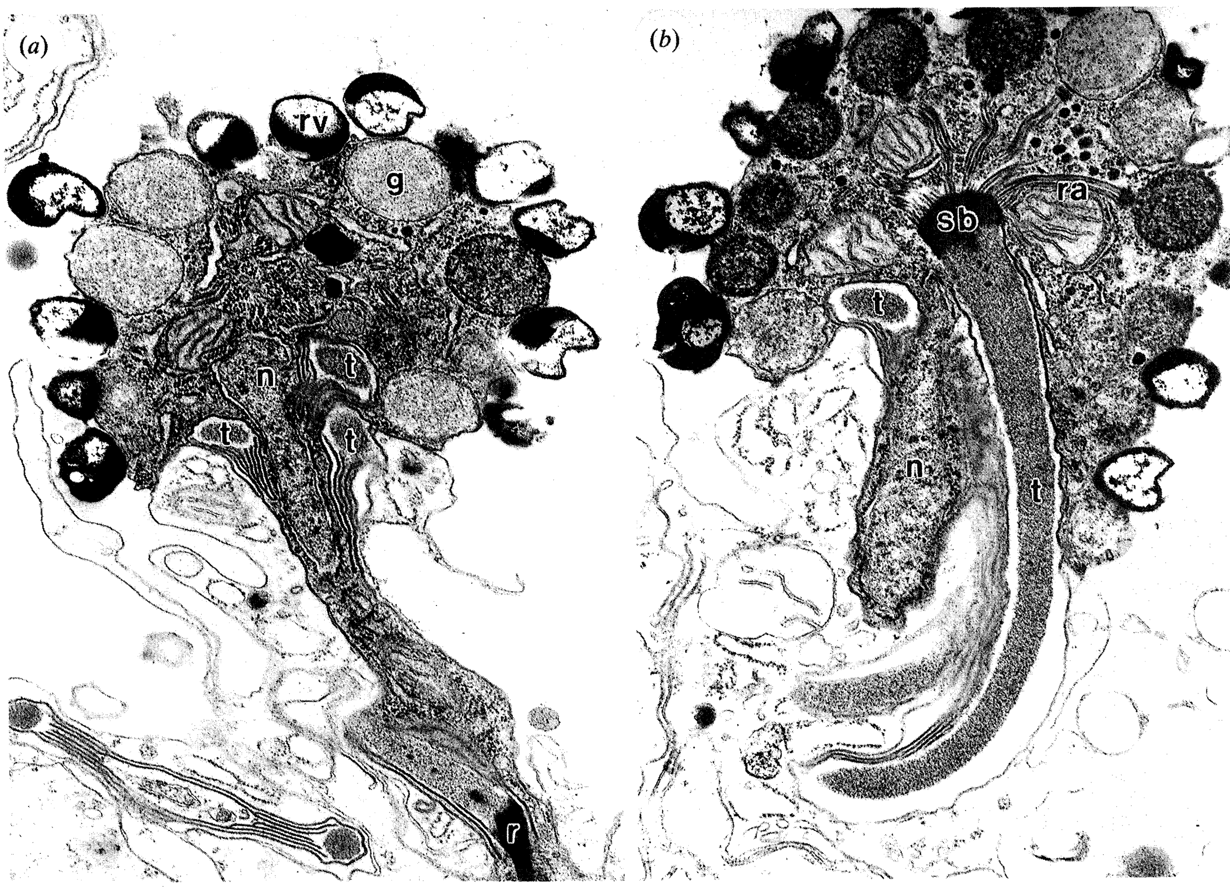

Figure 4. Type II colloblasts. (*a*) Parasagittal section. Note dense external granules (rv) and the spirals (t) of the filament around the nucleus (n). × 18 000. (*b*) Longitudinal section through the straight axial portion of the filament (t). Radii (ra) are often wavy. × 18 000.

light microscopy. They have a hemispherical collosphere 3.5 μm in diameter, with a collopod (figure 5*a*,*d*). The collosphere is covered with clear external granules 0.5 μm diameter (figure 5*a*,*b*). The internal granules are 0.7 μm in diameter and have a denser central zone (figure 5*b*,*c*). They are again linked to the spheroidal body by rectilinear filamentous radii. The cytoplasm between the radii contains many mitochondria but is not dense, distinguishing type III from type I and II colloblasts (figure 5*b*,*c*).

A filament runs along the main axis of the cell, starting from beneath the spheroidal body by the side of the nucleus (figure 5*a*,*d*). It has an opaque centre surrounded by MT (five or six depending on the cell) and is enveloped by a complex infolding of the plasma membrane (figure 5*f*,*g*). This groove of folded membrane also starts beneath the spheroidal body and has two or three folds running along its length. The filament makes a short side-loop (at the level of the stalk) covered by the adjacent cells (figures 2(III) and 5*d*). It is effectively exterior to the colloblast but remains linked by the membrane fold, and is overlain by the membrane of the adjacent cells. It then comes back into the collosphere, straightens up and finishes at a non-striated rootlet (figure 5*e*,*h*).

(*d*) ***Type IV colloblasts*** (figures 2 and 6)

Type IV colloblasts are found along with those of type V at the end of the tentilla. Their collospheres are 10 μm in diameter and lack external granules (figure 6*a*). They have characteristic, very large (2–2.5 μm) internal granules. These are kidney-shaped and are structured internally (figure 6*b*). Each granule is linked to the spheroidal body by a wavy radius composed of filamentous sub-units (figure 6*b*–*d*). Between the radii are many MT (figure 6*d*). The spheroidal body, lying in a dimple at the tip of the nucleus, is small and very dense (figure 6*a*). A filament starts from the spheroidal body (figure 6*a*,*c*) and immediately spirals 13–15 times, outlining a heart-shaped region. Then a last spiral, much less tight, runs around the collopod and ends in a short non-striated rootlet (figure 6*a*,*g*,*h*). All along its length, the filament has a dense core surrounded by MT. The number of MT varies between cells (seven to ten) but remains constant along the length of each filament (figure 6*f*). The filament is 0.25 μm in diameter, except for the first spiral (0.6 μm). The folds of membrane that envelop it, are very deep and oriented towards the nucleus (figure 6*f*). The last six or seven spirals lie at the cell periphery and deform the outline of the cell (figure 6*g*).

(*e*) ***Type V colloblasts*** (figures 2, 7)

These are relatively large (7 μm diameter collosphere, total height, 10–12 μm). Like those of type IV, they have no external granules (figure 7*a*,*b*). The spherical internal granules are dense and homoge-

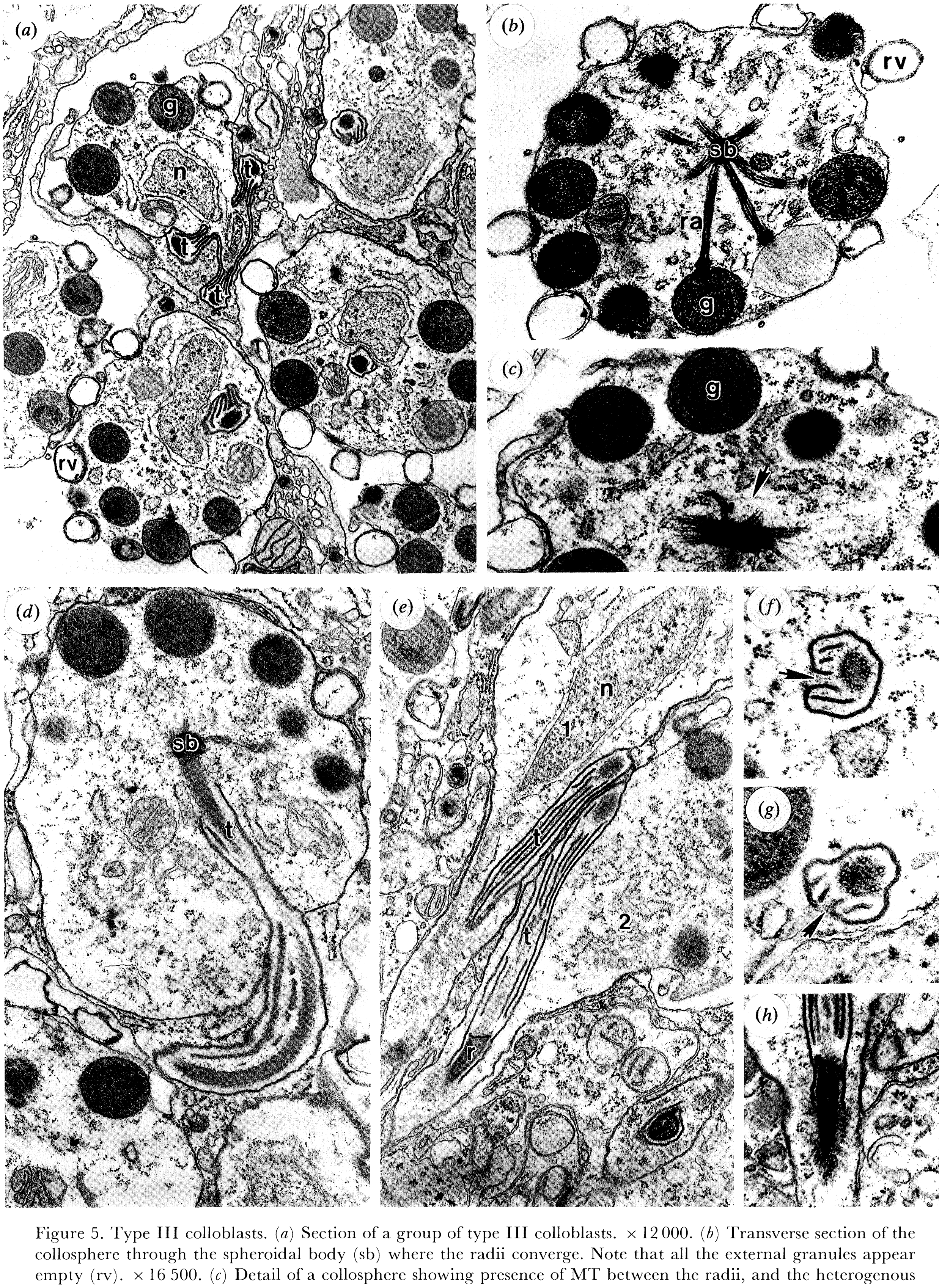

Figure 5. Type III colloblasts. (*a*) Section of a group of type III colloblasts. × 12 000. (*b*) Transverse section of the collosphere through the spheroidal body (sb) where the radii converge. Note that all the external granules appear empty (rv). × 16 500. (*c*) Detail of a collosphere showing presence of MT between the radii, and the heterogenous structure of the internal granules (g). × 21 000. (*d*) Longitudinal section: after a straight part the filament shows a side loop included in the neighbouring cells. × 16 500. (*e*) Terminal part of the filament (t) in two colloblasts (1 and 2); after a side loop, each filament enters the collopod and ends with a root (r). × 16 500. (*f,g*) Transverse section in the axial part of the filament. The number of MT can vary (six and five respectively in these cells). × 34 500 and × 39 000. (*h*) Detail of a root showing absence of transverse striation. × 23 500.

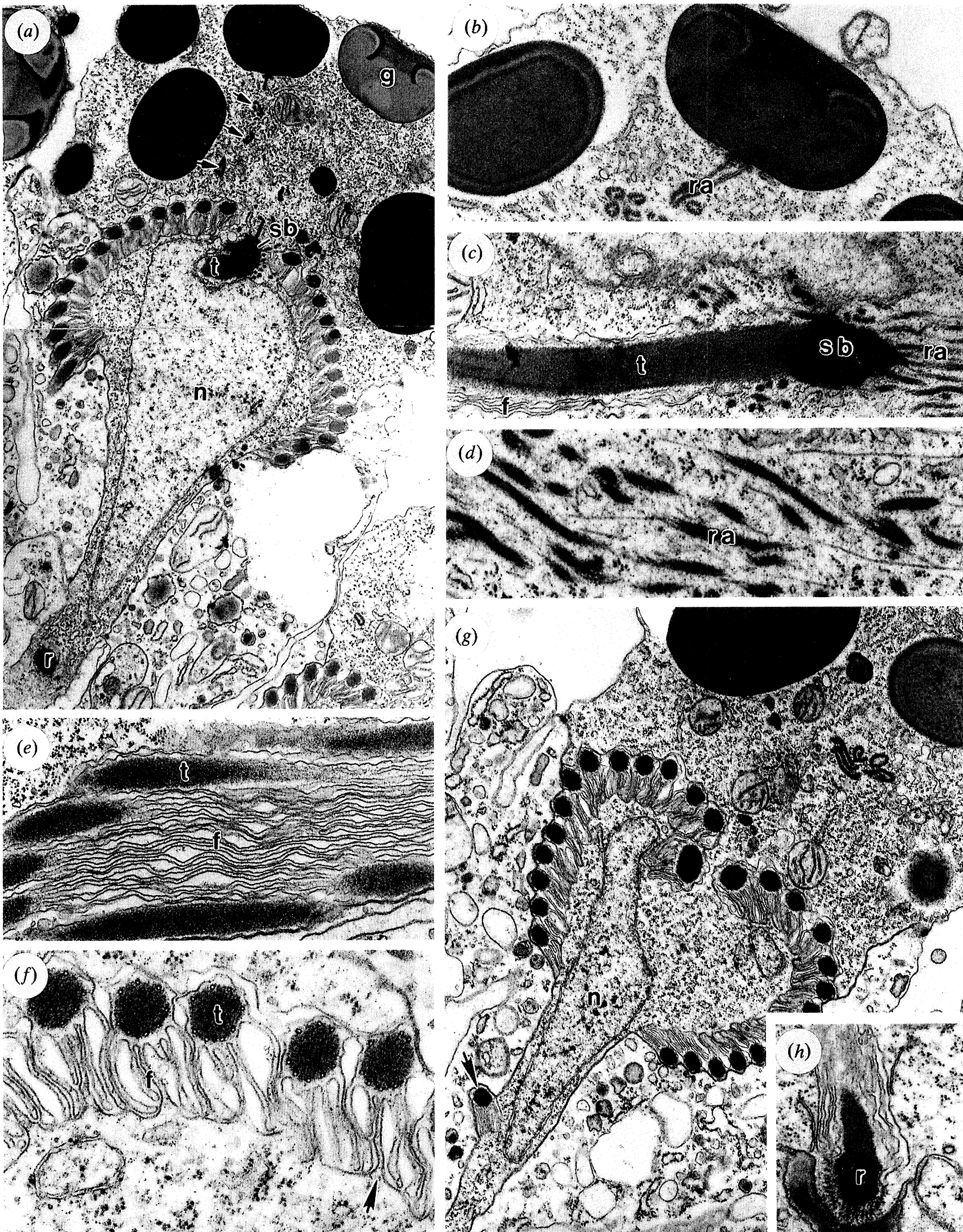

Figure 6. Type IV colloblasts. (*a*) Longitudinal section. Note the absence of external granules and the kidney-shaped internal granules (g). Only short sections of the wavy radii lie in this section (arrows). Beneath the spheroidal body (sb) the filament turns immediately to form a stack of spirals (13 in this case). × 8000. (*b*) Details of internal granules. × 16 500. (*c*) Beginning of the filament (t) beneath the spheroidal body (sb) where the radii converge. × 15 500. (*d*) Only short stretches of each wavy radius (ra) lie in the section. Note the MT. × 15 500. (*e*) Tangential section at the internal surface of the spirals and passing by the filament (t) and the membrane groove folds (f). × 19 500. (*f*) Transverse section of a filament (t) surrounded by eight MT. Note the opening of the membrane groove into the cytoplasm (arrow). × 34 500. (*g*) Longitudinal section showing the last spiral (arrow) around the collopod. × 10 000. (*h*) Detail of the root at the end of the filament. Note absence of striation. × 16 500.

nous. They are 1 μm in diameter and are pushed up against the plasma membrane at the top of the colloblasts (figure 7*b*). Only this region of the cell is exposed at the surface of the tentacle, the rest is surrounded by neighbouring sensory and epithelial cells (figure 7*b*). Each internal granule is linked by a wavy radius composed of a twisted filamentous subunit (figure 7*c*,*d*) to the spheroidal body in a dimple of the nucleus (figure 7*a*). The filament extends from the spheroidal body (figure 7*b*), and makes 9–10 tight spirals. The diameter increases until the seventh or eigth spiral and then decreases, finishing with a loose last spiral running around the collopod and ending in a non-striated rootlet (figure 7*a*,*b*). The filament core (0.2 μm in diameter) is dense with 5–7 peripheral MT (figure 7*e*,*f*). The deep folds in the surrounding plasma membrane are oriented towards the filament core.

(*f*) *Colloblast differentiation* (figures 8 and 9)

We examined differentiating colloblasts to see if the characteristics we noted in mature cells (absence of external granules in type IV and V for example) were always present, and to help interpreting certain structures, in particular the filament and spheroidal body.

(i) *External granules*

Colloblasts of type I, II and III are found developing in parallel groups. Each group is partially enveloped by an accessory gland cell, with a single accessory cell covering several colloblasts (figure 8*a*). These cells secrete granules which become arranged progressively in a layer around each collosphere, constituting the layer of external granules seen in mature colloblasts.

Type IV and V colloblasts also arise in groups in the tentacle bulbs but are never associated with gland cells capable of secreting external granules (figure 8*b*).

(ii) *Internal granules*

Internal granules, both fully formed and in the process of formation by fusion of Golgi vesicles (figure 8*b*), can be seen in differentiating cells. The developing internal granules each have a distinct region where the radii will eventually become attached (figure 8*c*). This zone may form anywhere on the surface of the granule. Its position is not related to the future centre of the collosphere.

(iii) *Filament, spheroidal body and radii*

In all five types of colloblast, the filament appears at the same time as the first granules. It first resembles a strand of dense material running from one pole of the cell to the other beneath the plasma membrane (figure 9*a*,*d*). The external membrane quickly forms two folds which envelop this strand and join up (figure 9*d*–*f*). At the same time, MT appear around the filament. The filament has not yet formed spirals at this stage. Its upper end is in contact with a small accumulation of dense material, the beginning of the spheroidal body (figure 9*a*) while the basal end differentiates into a root (figure 9*b*). Later the filament lengthens and forms spiral. This process is easily observed in type IV and V, where many spirals are put into place one after the other (figure 9*d*–*l*). In sections each spiral first appears against the plasma membrane. Then, in type IV and V colloblasts, the first spirals migrate towards the centre of the collosphere, carrying the plasma membrane with them and so forming deep folds (figures 6*a* and 8*b*).

In transverse sections, the colloblast filament has a ring of peripheral MT. We followed the arrangement, number and development of these MT during the formation of each colloblast type. The number of MT along a filament varies from one type of colloblast to another and may also vary within one type of colloblast. Thus, type I has between nine and 11 (figure 3*d*,*e*), type III has between five and six (figure 5*f*,*g*), type IV has between seven and ten (figure 9*f*–*l*) and type V has between five and seven (figure 7*e*,*f*). In a single colloblast the number of MT is always the same, both in the initial stage of development, when only a straight filament is present and when mature with a fully formed filament. Thus, the number of MT is not related to developmental stage.

In mature colloblasts, the spheroidal body lies near the nucleus (figure 3*h*) sometimes lodged in a dimple in the nucleus (figure 7*a*). During the formation of the five type of colloblasts of *Minictena luteola*, the developing spheroidal body becomes located at the future centre of the collosphere, at one end of the filament, while at the same stage, the nucleus lies at the opposite pole of the cell (figure 8*a*). It is later that the nucleus becomes elongated and pulled towards the spheroidal body to meet it. This presumptive spheroidal body could represent a nucleation centre for the MT of the filament or act to organize the structure of the collosphere. The radii which develop on each internal granule start with random orientation (figure 8*d*) depending on where their fixation has arisen earlier (figure 8*c*). Later, they all converge at the presumptive spheroidal body. Each developing radius has a dense swelling at its free end which contributes to the formation of the spheroidal body as it fuses at the centre. (figure 8*d*–*f*).

4. DISCUSSION AND CONCLUSION

This is the first time that polymorphism has been observed among the colloblasts arming the tentacles of a ctenophore. This is comparable to the diversity that exists between the different categories of cnidocysts along the tentacles of cnidarians.

Benwitz (1978), Franc (1978) and Mackie *et al.* (1988) established that a layer of external granules is secreted by glandular accessory cells. In *Minictena luteola*, the type I, II and III colloblasts are indeed associated with a gland cell during development and this cell degenerates after having formed a layer of external granules. In contrast, type IV and V colloblasts are never associated with an accessory cell and have no external granules when mature. The existence of colloblasts with internal granules only supports the hypothesis of Weill (1935), Hovasse & de Puytorac

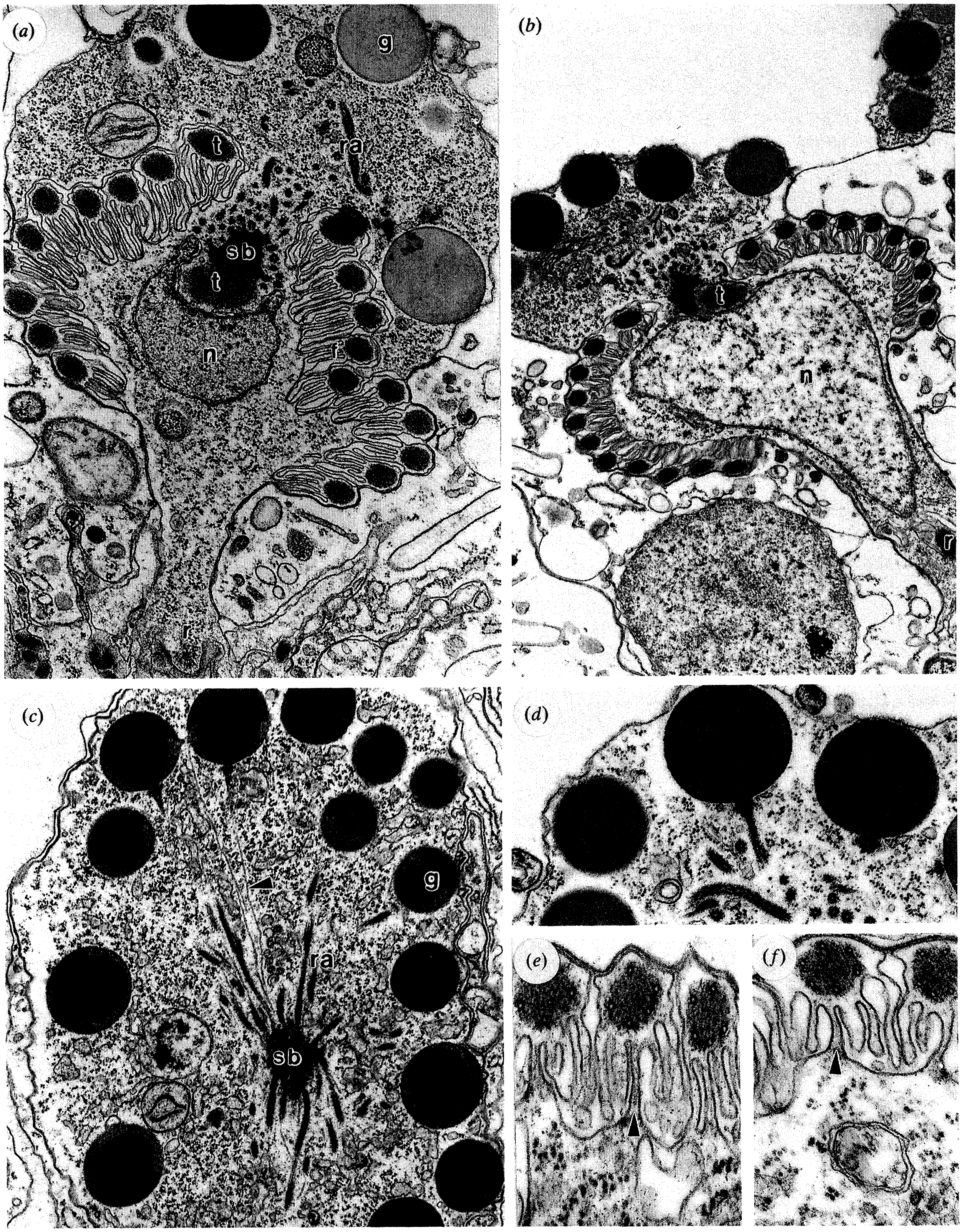

Figure 7. Type V colloblasts. (*a*) Longitudinal section. Note absence of external granules and the spherical form of the internal granules (g). The radii are very wavy so appear in short length. × 14 500. (*b*) Longitudinal section beneath the spheroidal body and showing the filament turning to form the first spiral, without an axial portion. × 11 000. (*c*) Transverse section of the collosphere at the level of spheroidal body (sb). Note the MT (arrow). × 14 000. (*d*) Detail of the internal granules and the radii. × 24 500. (*e,f*) Transverse sections in the spirals of two mature colloblasts. The number of MT varies from one colloblast to another (five and six here) and the membrane groove is still open to the cytoplasm (arrow). × 49 000 and × 41 000.

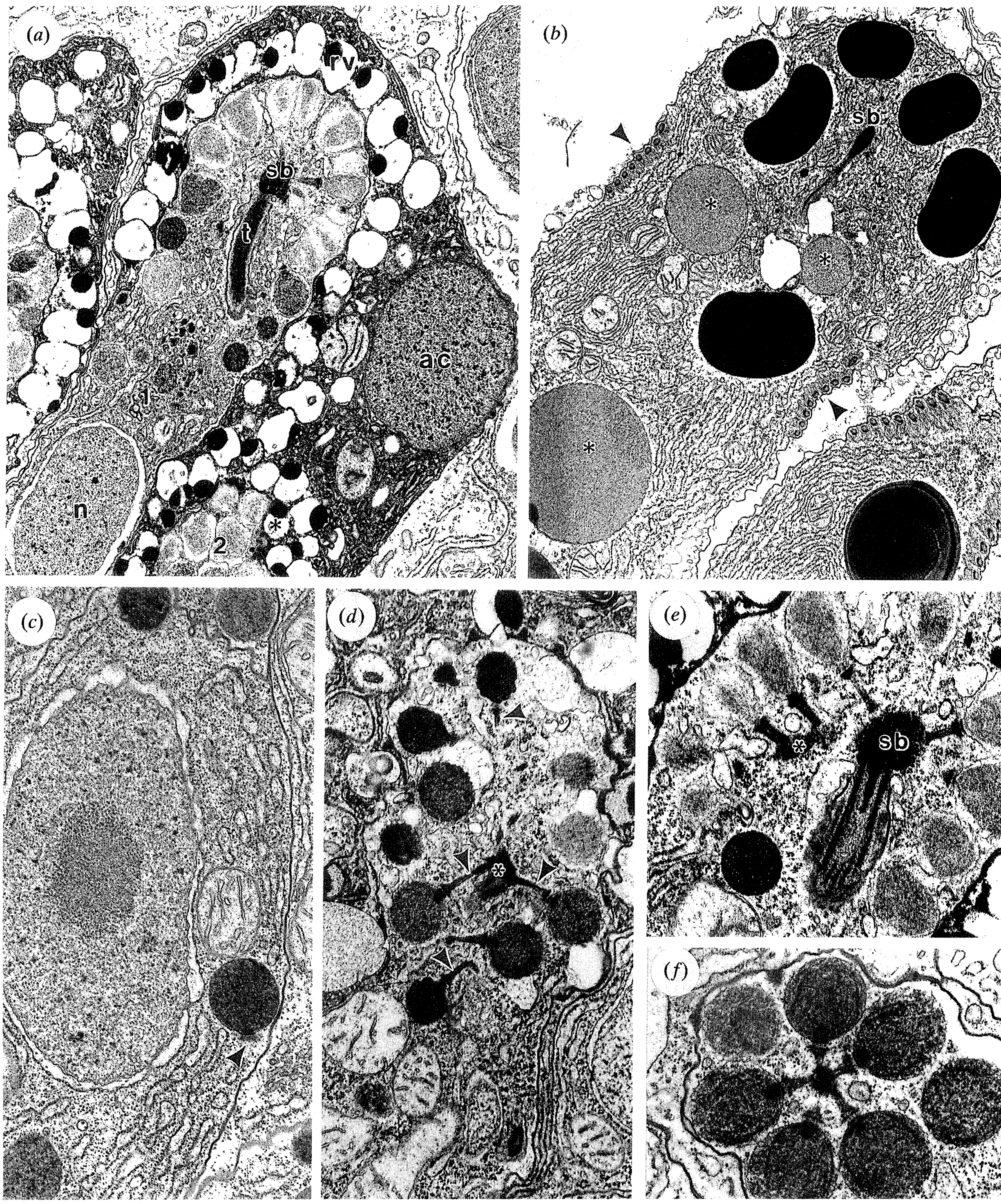

Figure 8. Colloblast differentiation. (*a*) Two differentiating type I colloblasts (1 and 2) in the tentacle base. A single accessory cell (ac) envelopes these two colloblasts and puts in place the external granule layer (rv). At this stage, the nucleus is far from the spheroidal body (sb). × 8000. (*b*) Type IV colloblasts during differentiation. Some granules are completely formed, others (*) are being secreted. The abundance of reticulum is characteristic of this stage of granule formation. The filament extending from the spheroidal body forms eight spirals (13 to 15 at the end of differentiation) in the middle part of the cell (arrow). × 6000. (*c*) Very young type I colloblast. Note beginning of a radius on a granule (arrow). × 14 500. (*d*) Type I colloblast showing random orientation of the radii, which later converge to participate in the formation of the spheroidal body (*). × 13 500. (*e*) The beginning of the spheroidal body forms close to the end of the filament (sb) and becomes enlarged by supply of dense material from the ends of the radii. These often aggregate (*) before fusing with the spheroidal body. × 13 500. (*f*) Formation of the spheroidal body in a type III colloblast. The radii are very short but will increase in length later. × 17 500.

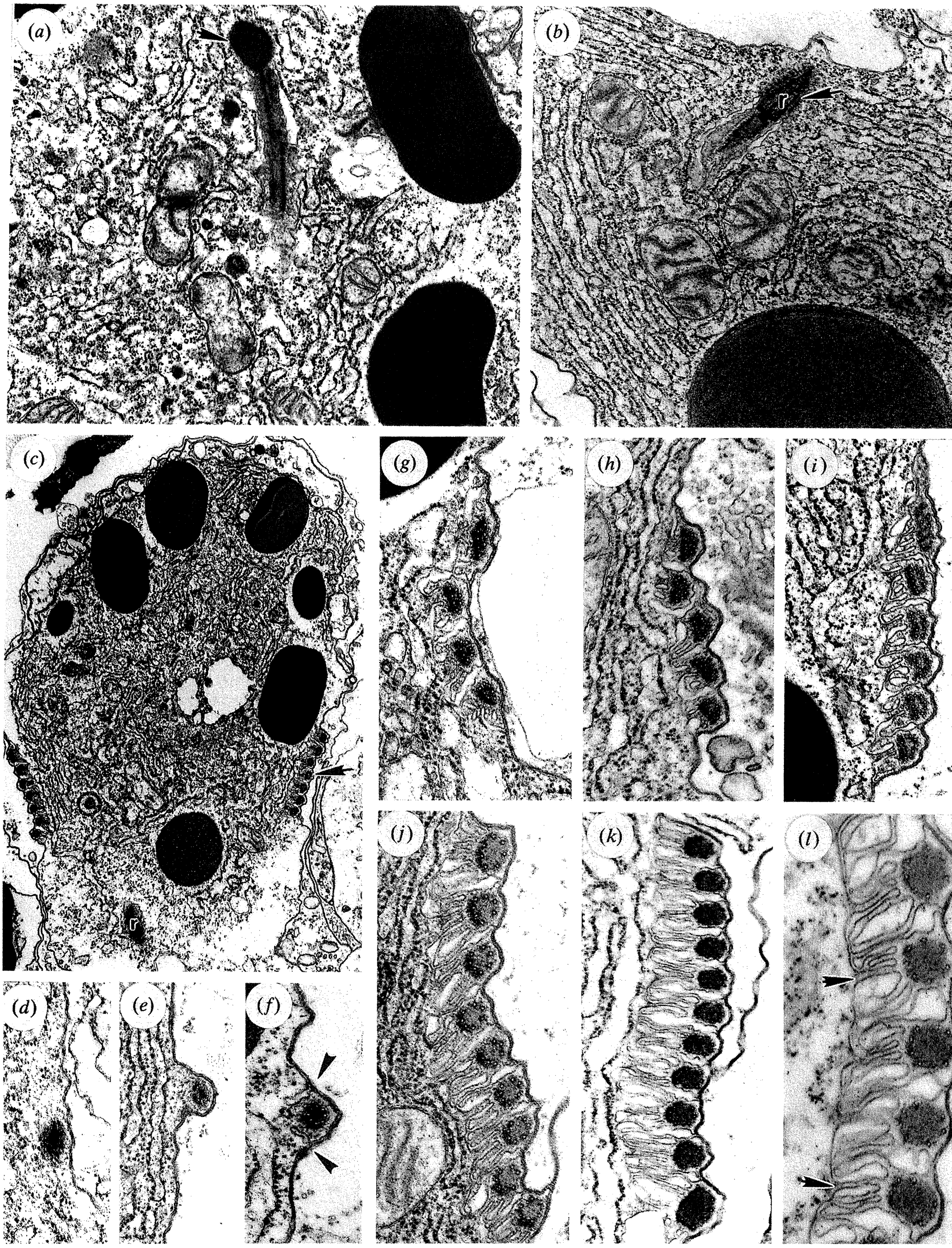

Figure 9. Type IV colloblasts differentiation. (*a*) The presumptive spheroidal body (arrow) at the top of the filament in a type IV colloblast. × 14 500. (*b*) Root forming at the end of a filament. The abundance of reticulum indicates an early stage. × 14 500. (*c*) Stage with seven spirals (arrow). Note the root (r). × 6000. (*d–f*) Stages with 1 spiral. Note in (*f*) two folds of the plasmic membrane and appearence of MT. × 23 500, × 24 500 and × 29 500. (*g–l*) Details of the progressive settling of the spirals of a type IV colloblast. Note that the number of MT is constant along a single filament, but varies from one colloblast to another, and seems independant of the stage. (*g*) Four spirals, seven MT. × 24 500. (*h*) Five spirals, nine MT. × 25 000. (*i*) Six spirals, ten MT. × 24 500. (*j*) nine spirals, seven MT. × 19 500. (*k*) 11 spirals, eight MT. × 24 500. (*l*) 15 spirals, seven MT (detail). × 34 500.

(1962) and Franc (1978), that external granules are not required for adhesion of prey to the tentacle.

The spheroidal body has consistently been described as being tightly apposed to the nucleus. It has thus even been considered to be a nuclear extrusion (Hovasse & de Puytorac 1962). Our examination of colloblast development in *M. luteola* shows that the two structures only become associated secondarily.

In all five types of colloblasts in *M. luteola*, only a single filament was found running from the spheroidal body to the base of the collopod. In type I, II and III, the filament has both straight axial portions and spiral portions. It is possible that the straight region corresponds to axial filament described by the first authors. In type IV and V colloblasts, the filament has only one spiral turn and cannot be confused with the nucleus which is usually pyramid shaped.

Storch & Lehnert-Moritz (1974) interpreted the filament as a modified axoneme whose MT disappear at the end of the cell differentiation. Benwitz (1978) observed nine MT along the filament and supported this idea. Several of our observations contradict this hypothesis. Firstly, MT doublets such as those seen in axonemes are never found. Secondly, in *M. luteola* the number of MT can be nine as observed by Benwitz (1978) in *Pleurobrachia*, but equally can be from five to 11. In *M. luteola*, the number of MT is restricted to within one or two MT for each type of colloblast. For a given colloblast, the MT number is constant. It is the same all along the filament and does not vary according to development stage. Thirdly, no axonemes have been described with a dense core comparable to that seen in the colloblast filament. Fourthly, we have never found centriolar structures at the base of the filament. Lastly, the root at the end of the filament only rarely has transverse striation such as is seen in ciliary rootlets (Benwitz 1978; Franc 1978).

All these characteristics indicates that the colloblast filament is a specialized structure distinct from an axoneme. The peripheral MT may be a guide or support during the morphogenesis of the filament and/or be important for its ultimate function. In *M. luteola* we have found MT persisting in mature colloblasts. Their function is unknown. The filament might actively uncoil once the colloblast has been used to capture prey or react like a spring and be pulled passively by the prey.

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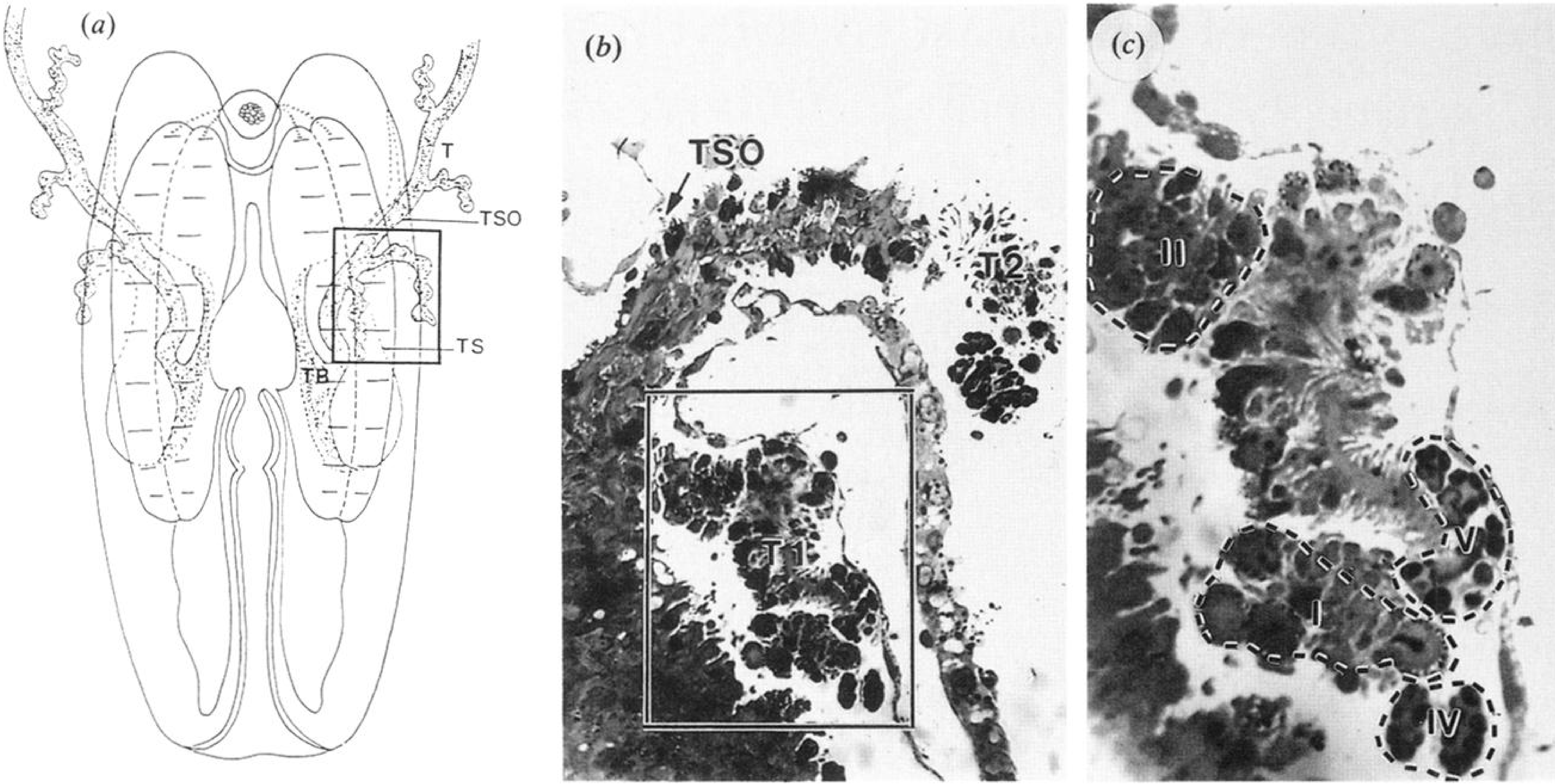

Figure 1. (*a*) Schematic diagram of *Minictena luteola* (tentacular plane) (1.5 mm). Tentacle (T) emerges from the tentacle sheath (TS); (TB, tentacle base; TSO, tentacle sheath opening). (*b*) Semi-thin section across two tentilla (T1 and T2) of the tentacle (T). (*c*) Tentilla T1 detail, colloblasts of one type are grouped together.

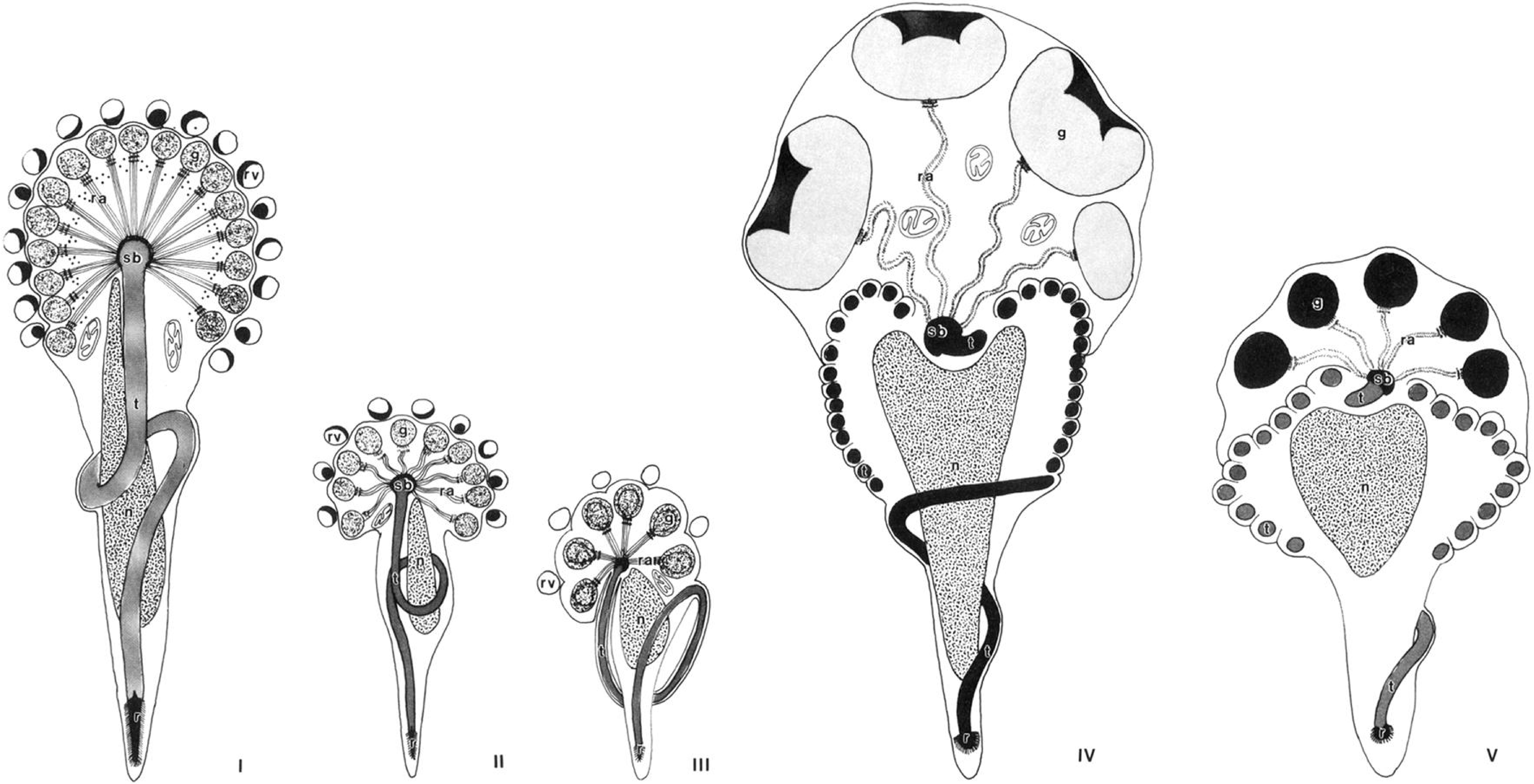

Figure 2. Types I to V colloblasts drawn to scale demonstrating their main features. The membrane grooves surrounding the filament and longitudinal MT are not shown. In types IV and V, the upper part of the filament is shown in section.

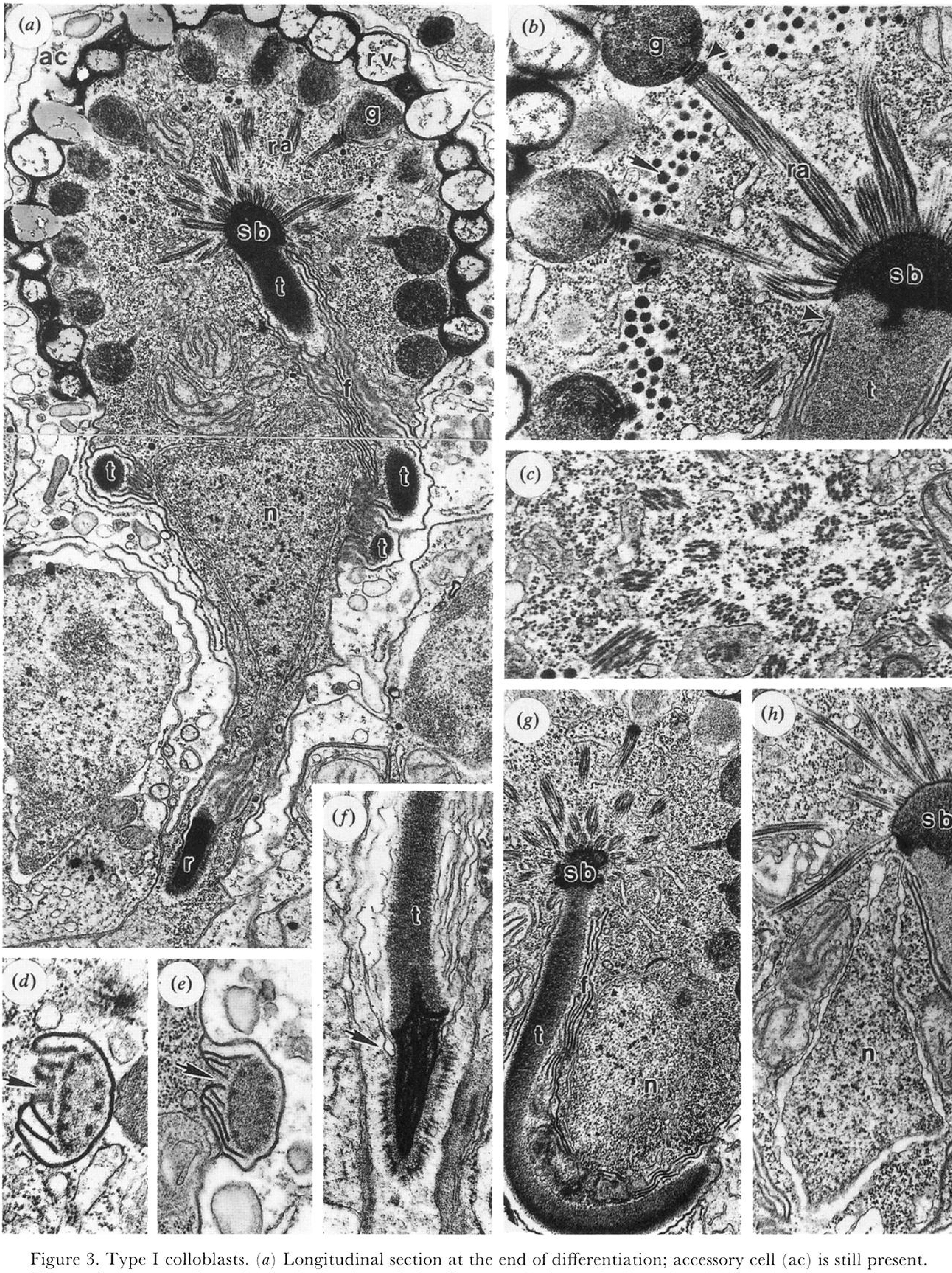

Figure 3. Type I colloblasts. (*a*) Longitudinal section at the end of differentiation; accessory cell (ac) is still present. The section passes through the beginning of the filament (t) beneath the spheroidal body (sb) and by the longitudinal folds (t) of the membranal groove surrounding the filament. Note the spirals cut transversally (t). ×13 500. (*b*) Collosphere detail: radii (ra) linking internal granules (g) to the spheroidal body (sb) are straight; they join the granules at a differentiated zone (upper arrow). Note the presence of opaque granulations (lower arrow). The membrane groove surrounding the filament starts beneath the spheroidal body. ×23 500. (*c*) Transverse section of radii. They are composed of two concentric filamentous cylinders. ×29 500. (*d*) Transverse section in the straight part of the filament. It is surrounded by nine MT. The enveloping membrane groove communicates with the cytoplasm (arrow). ×34 500. (*e*) Transverse section of the spiral part of a filament surrounded by ten MT. Communication with the colloblast cytoplasm (arrow) is maintained. ×24 500. (*f*) Root at the end of the filament. Note the absence of transverse striations and the end of membrane groove above the root (arrow). ×29 500. (*g*) Longitudinal section showing continuity between the axial straight portion and the spiral portion of the filament. ×12 000. (*h*) Spheroidal body–nucleus junction. The apex of the nucleus (n) is in contact with the spheroidal body but the nuclear membrane is intact. ×16 500.

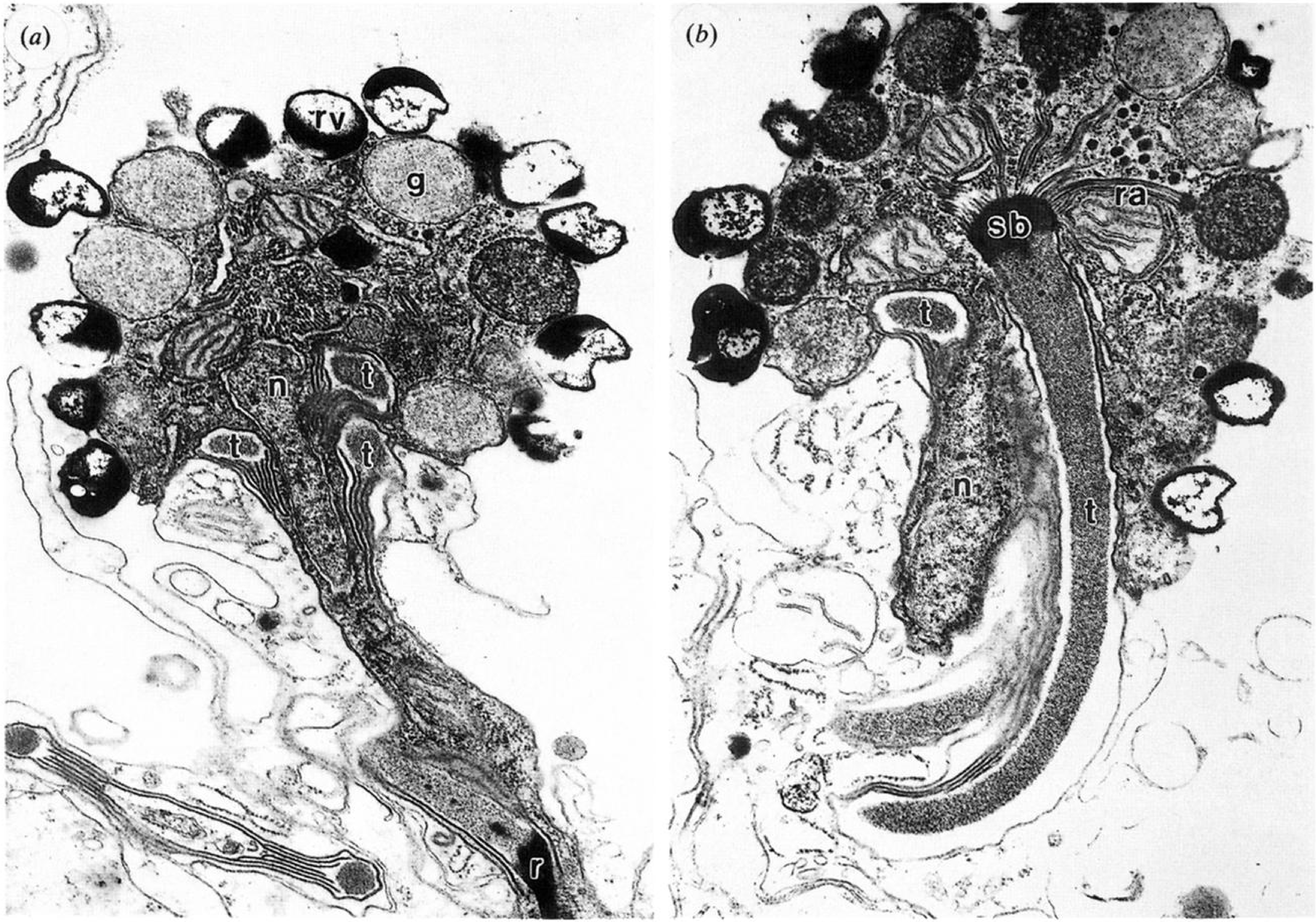

Figure 4. Type II colloblasts. (*a*) Parasagittal section. Note dense external granules (rv) and the spirals (t) of the filament around the nucleus (n). × 18 000. (*b*) Longitudinal section through the straight axial portion of the filament (t). Radii (ra) are often wavy. × 18 000.

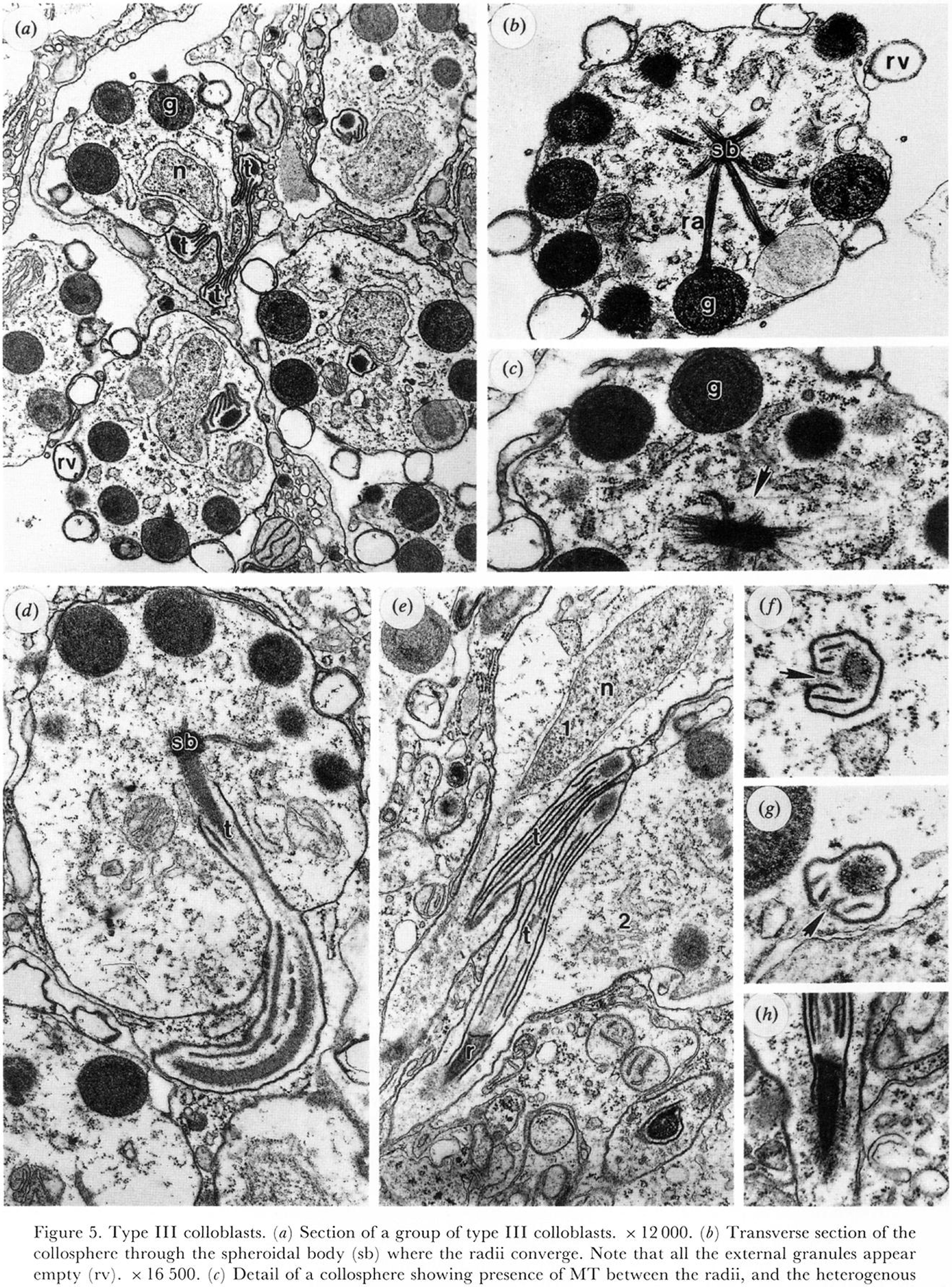

Figure 5. Type III colloblasts. (*a*) Section of a group of type III colloblasts. × 12 000. (*b*) Transverse section of the collosphere through the spheroidal body (sb) where the radii converge. Note that all the external granules appear empty (rv). × 16 500. (*c*) Detail of a collosphere showing presence of MT between the radii, and the heterogenous structure of the internal granules (g). × 21 000. (*d*) Longitudinal section: after a straight part the filament shows a side loop included in the neighbouring cells. × 16 500. (*e*) Terminal part of the filament (t) in two colloblasts (1 and 2); after a side loop, each filament enters the collopod and ends with a root (r). × 16 500. (*f,g*) Transverse section in the axial part of the filament. The number of MT can vary (six and five respectively in these cells). × 34 500 and × 39 000. (*h*) Detail of a root showing absence of transverse striation. × 23 500.

Figure 6. Type IV colloblasts. (*a*) Longitudinal section. Note the absence of external granules and the kidney-shaped internal granules (g). Only short sections of the wavy radii lie in this section (arrows). Beneath the spheroidal body (sb) the filament turns immediately to form a stack of spirals (13 in this case). × 8000. (*b*) Details of internal granules. × 16 500. (*c*) Beginning of the filament (t) beneath the spheroidal body (sb) where the radii converge. × 15 500. (*d*) Only short stretches of each wavy radius (ra) lie in the section. Note the MT. × 15 500. (*e*) Tangential section at the internal surface of the spirals and passing by the filament (t) and the membrane groove folds (f). × 19 500. (*f*) Transverse section of a filament (t) surrounded by eight MT. Note the opening of the membrane groove into the cytoplasm (arrow). × 34 500. (*g*) Longitudinal section showing the last spiral (arrow) around the collopod. × 10 000. (*h*) Detail of the root at the end of the filament. Note absence of striation. × 16 500.

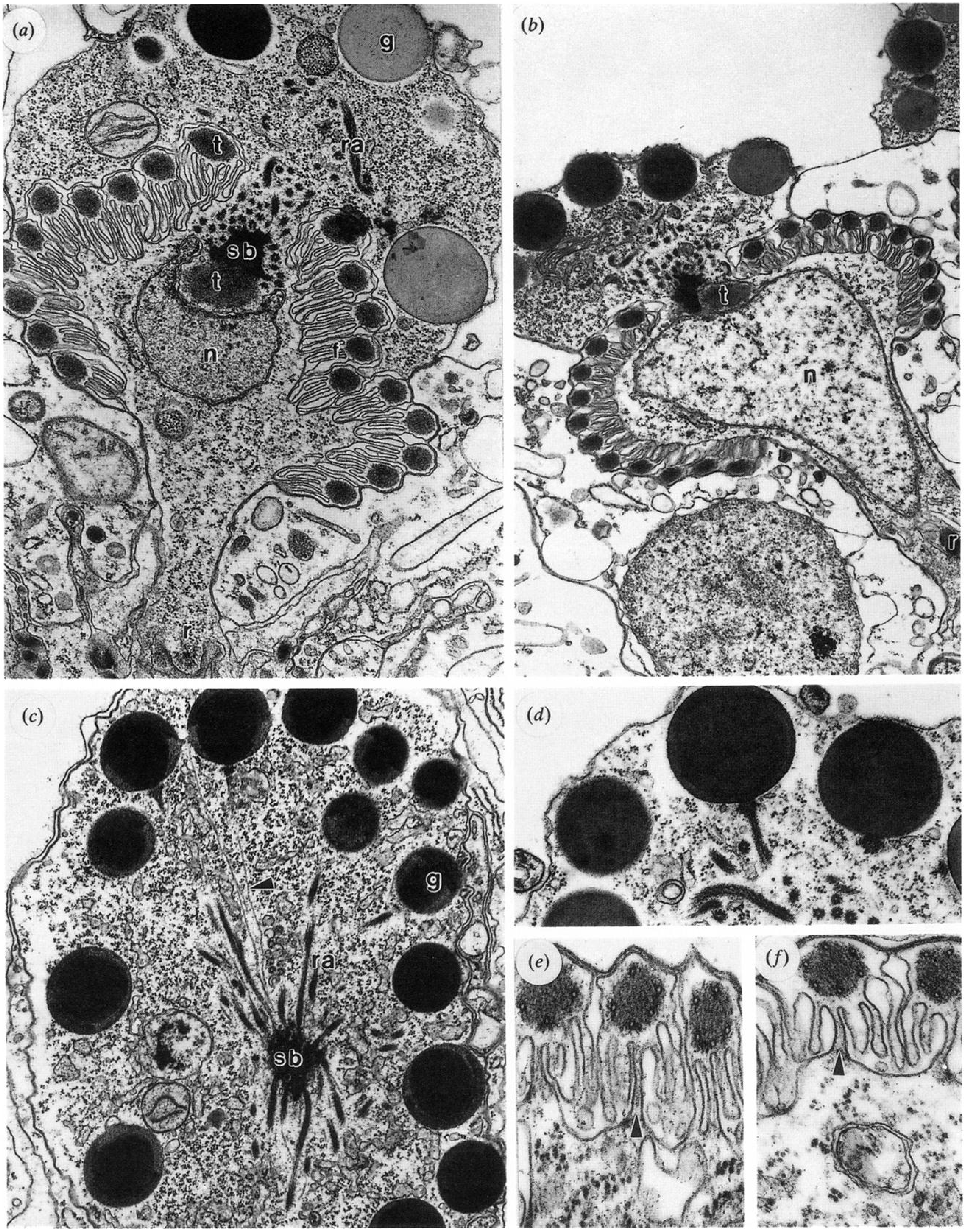

Figure 7. Type V colloblasts. (*a*) Longitudinal section. Note absence of external granules and the spherical form of the internal granules (g). The radii are very wavy so appear in short length. × 14 500. (*b*) Longitudinal section beneath the spheroidal body and showing the filament turning to form the first spiral, without an axial portion. × 11 000. (*c*) Transverse section of the collosphere at the level of spheroidal body (sb). Note the MT (arrow). × 14 000. (*d*) Detail of the internal granules and the radii. × 24 500. (*e,f*) Transverse sections in the spirals of two mature colloblasts. The number of MT varies from one colloblast to another (five and six here) and the membrane groove is still open to the cytoplasm (arrow). × 49 000 and × 41 000.

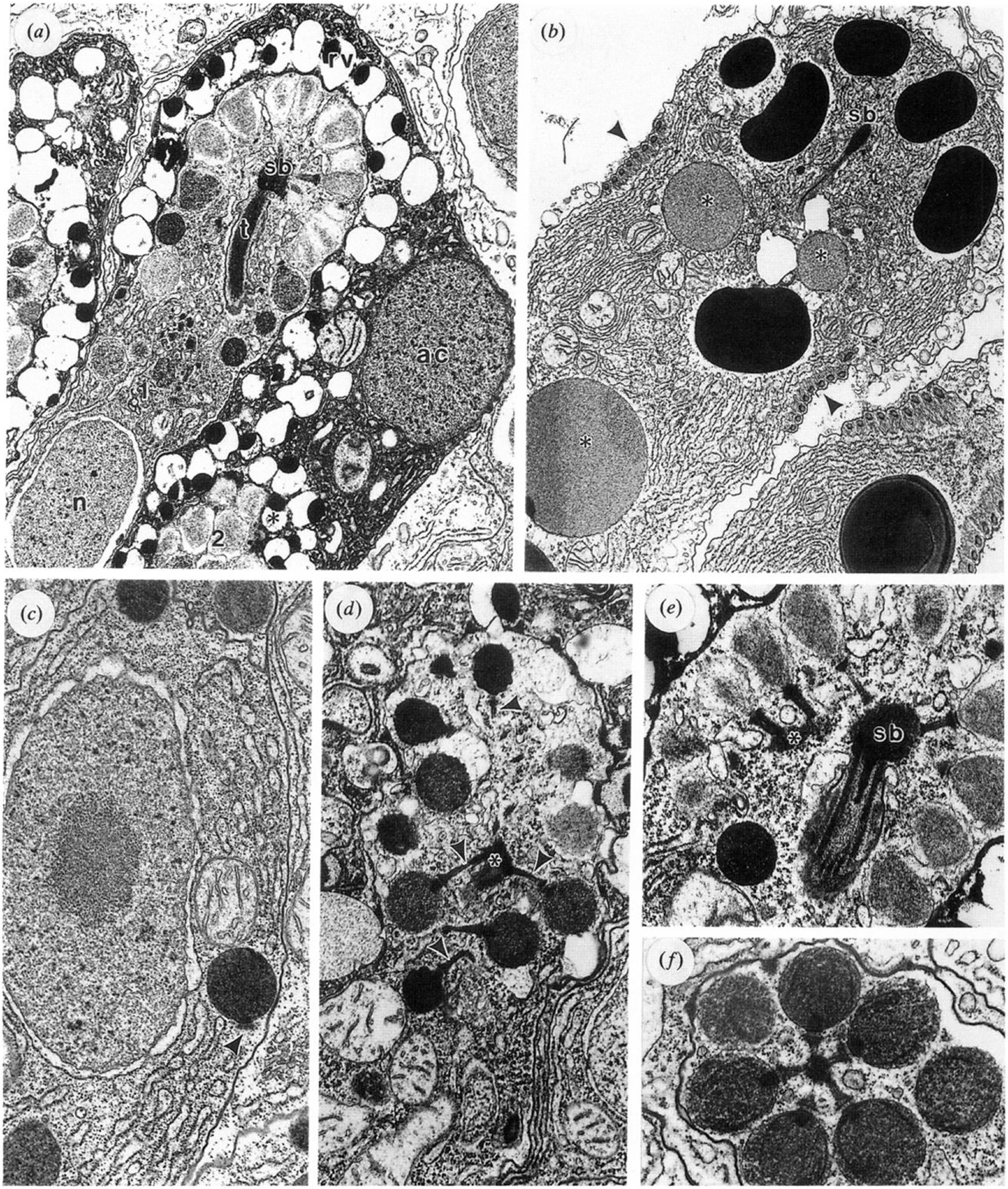

Figure 8. Colloblast differentiation. (*a*) Two differentiating type I colloblasts (1 and 2) in the tentacle base. A single accessory cell (ac) envelopes these two colloblasts and puts in place the external granule layer (rv). At this stage, the nucleus is far from the spheroidal body (sb). × 8000. (*b*) Type IV colloblasts during differentiation. Some granules are completely formed, others (*) are being secreted. The abundance of reticulum is characteristic of this stage of granule formation. The filament extending from the spheroidal body forms eight spirals (13 to 15 at the end of differentiation) in the middle part of the cell (arrow). × 6000. (*c*) Very young type I colloblast. Note beginning of a radius on a granule (arrow). × 14 500. (*d*) Type I colloblast showing random orientation of the radii, which later converge to participate in the formation of the spheroidal body (*). × 13 500. (*e*) The beginning of the spheroidal body forms close to the end of the filament (sb) and becomes enlarged by supply of dense material from the ends of the radii. These often aggregate (*) before fusing with the spheroidal body. × 13 500. (*f*) Formation of the spheroidal body in a type III colloblast. The radii are very short but will increase in length later. × 17 500.

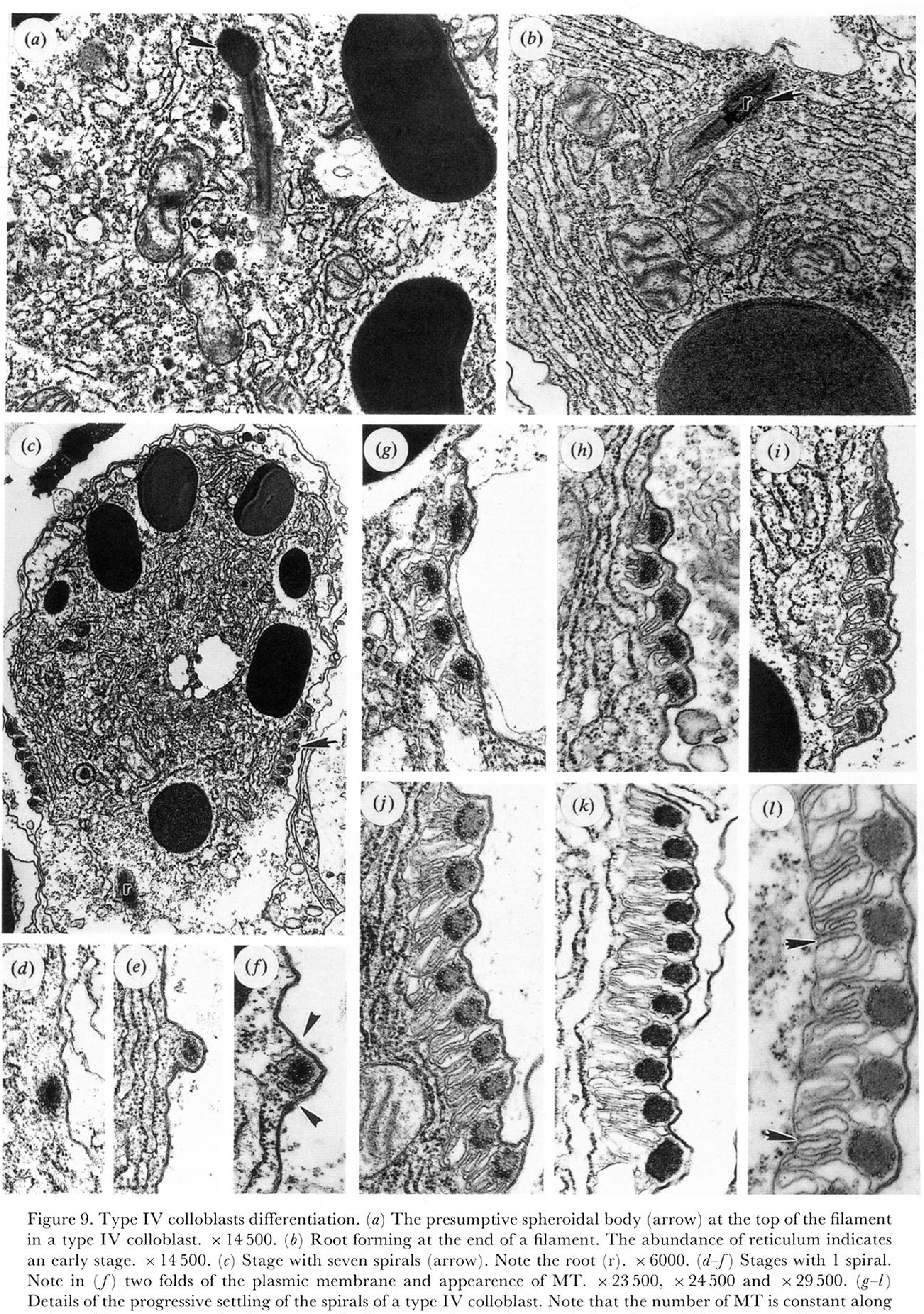

Figure 9. Type IV colloblasts differentiation. (*a*) The presumptive spheroidal body (arrow) at the top of the filament in a type IV colloblast. × 14 500. (*b*) Root forming at the end of a filament. The abundance of reticulum indicates an early stage. × 14 500. (*c*) Stage with seven spirals (arrow). Note the root (r). × 6000. (*d–f*) Stages with 1 spiral. Note in (*f*) two folds of the plasmic membrane and appearence of MT. × 23 500, × 24 500 and × 29 500. (*g–l*) Details of the progressive settling of the spirals of a type IV colloblast. Note that the number of MT is constant along a single filament, but varies from one colloblast to another, and seems independant of the stage. (*g*) Four spirals, seven MT. × 24 500. (*h*) Five spirals, nine MT. × 25 000. (*i*) Six spirals, ten MT. × 24 500. (*j*) nine spirals, seven MT. × 19 500. (*k*) 11 spirals, eight MT. × 24 500. (*l*) 15 spirals, seven MT (detail). × 34 500.