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Morphological specializations: Ultrastructural

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In accordance with the special functional properties of the autonomously contractile veins in the wing membrane of Chiroptera, which have been demonstrated comprehensively in the works of Mislin[1-3], the electron microscopical studies of this organ in the flying fox, *Pteropus vampyrus* (Gray) and the bat *Myotis myotis* (Borkhausen) show some remarkable ultrastructural specializations of the vessel structure. These vascular specializations concern particularly the endothelium as well as the vascular smooth muscle and its innervation.

The general morphology of the 120-µm thick vessel wall is in accordance with that of other mammalian veins[4]. It is characterized by a tunica intima with an always closed endothelium layer, associated with collagenous fibres, few elastic structures but without smooth muscle cells. The following layer, the tunica media, is built up of only circular muscle cells which are surrounded by a fine network of collagenous fibres. The tunica adventitia contains few muscles and consists of a network of collagenous fibres, corresponding to those of the media in which in addition to the vasa vasorum may non-myelinated nerve fibres can be seen. These fibres have contact with the peripheral muscle cells of the tunica media.

The most prominent endothelial specializations of this contractile vessel are the many unipolar branched processes in the abluminal side of the cells. They have a length up to 10 µm and their terminal branches are fixed in the collagenous and elastic tissue marking the border between the tunica intima and media so that the endothelium has an arcade-like appearance (figure 1, a). Depending on the contractile state of the vessel, the distance of these arcades to the muscle tissue of the media changes. The degree of flexure of the central cell area expresses the high degree of adaptability of this layer to the considerable variations of the vessel lumen. According to the changeable tensile stress, the cytoplasm of the endothelial cells contain filamentous structures such as we see in other contractile vessels[4-7]. It is not yet clarified, whether these structures function as contractile myofilaments like the actin-myosin-system of muscle cells or solely as stabilizing elements. The functional importance of the intraplasmatic, lysosome-like dense bodies is also not yet known[8].

The spindle-like muscle cells of tunica media - building up 5-6 layers - show very close side-to-side interdigitations[4] (figure 1, b). As in other smooth muscle cells[9-11] we can distinguish 2 sets of myofilaments with diameters of 70 Å respectively 100 Å and dense patches or dense bodies in which the thin filaments insert (figures 1, c and 2, b). They appear to have a function similar to that of the Z-lines of striated muscle, with a sliding filament mechanism of contraction in which thick (myosin) and thin (actin) filaments slide relative to each other. In the peripheral sarcolemm the thin filaments are inserted by hemidesmosome-like structures (figure 2, e).

A very prominent feature of these vascular muscle cells is the significantly greater content of mitochondria than in non-autonomously contractile vessels (figure 1, c and 2, a). As in the muscle cells of other autonomously contractile blood and lymph vessels[4], we can see large accumulations of these organells (30-40) near the centrally situated nucleus and in streaks between the contractile apparatus reaching up to the cell surface. There they are associated with micropinocytotical vesicles, free ribosomes, glycogen particles, granular or lamellated dense bodies and a well developed sarcoplasmatic reticulum, generally of the smooth form (figure 2, d and e). More or less straight

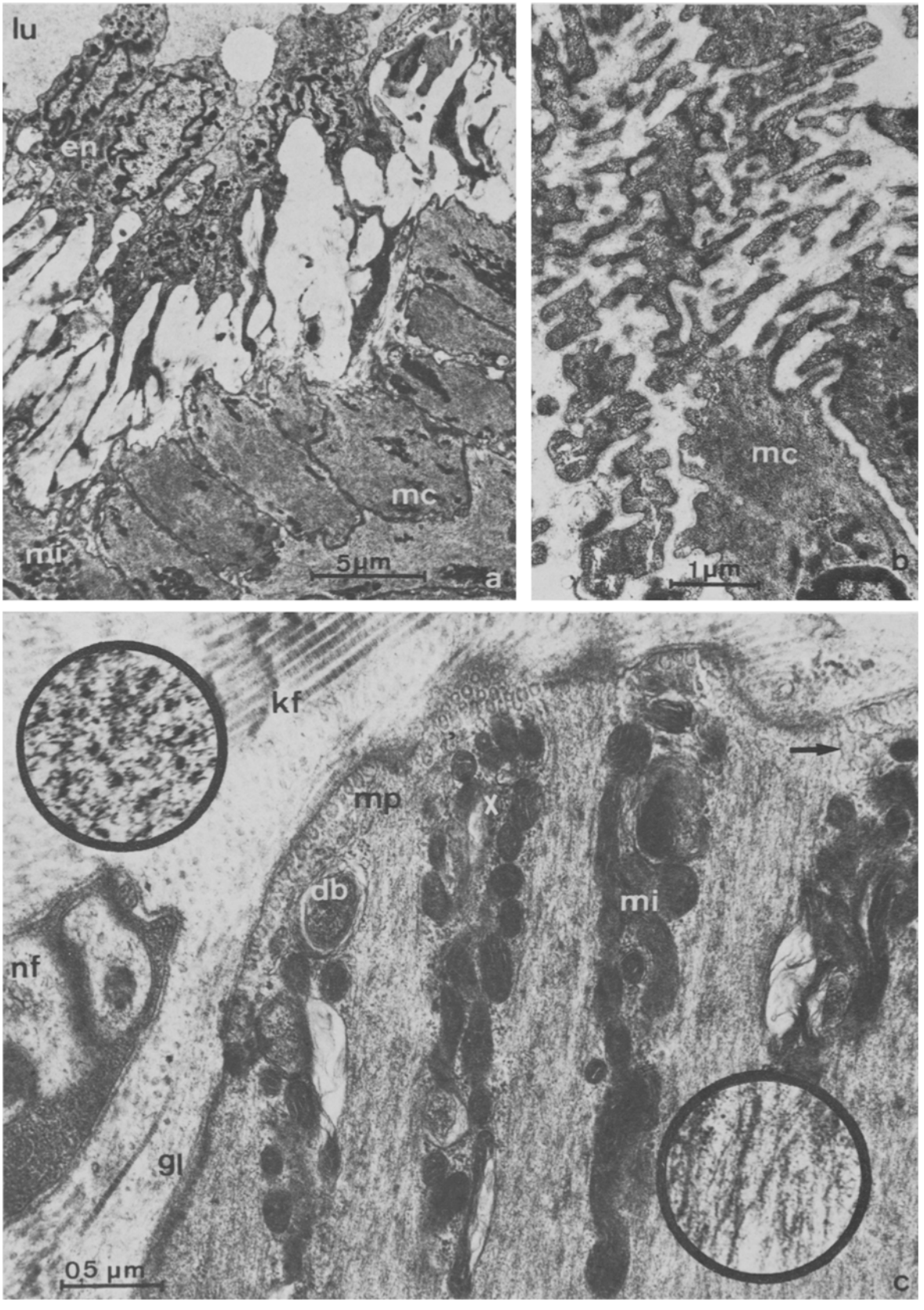

Fig. 1. *a* Inner area of an autonomously contractile vein of the wing-membrane of Pteropus with an arcade-like endothelium (en); *b* muscle cell (mc) of the patagium vein of *Myotis* with numerous interdigitated processes; *c* muscle cell of the peripheral t. media (*Pteropus*-vein) shows streaks of electron dense sarcosomes (mi) associated with micropinocytotic vesicles (mp) of the sarcolemm; 2 sets of myofilaments can be identified in cross and longitudinal sections (left resp. right inset); lumen (lu), nerve fibre (nf), collagenous fibre (kf), glycocalix (gl), dense body (db), glycogen (x), further explanations see in text; magnifications: × 54,000 (left inset), × 44,000 (right inset).

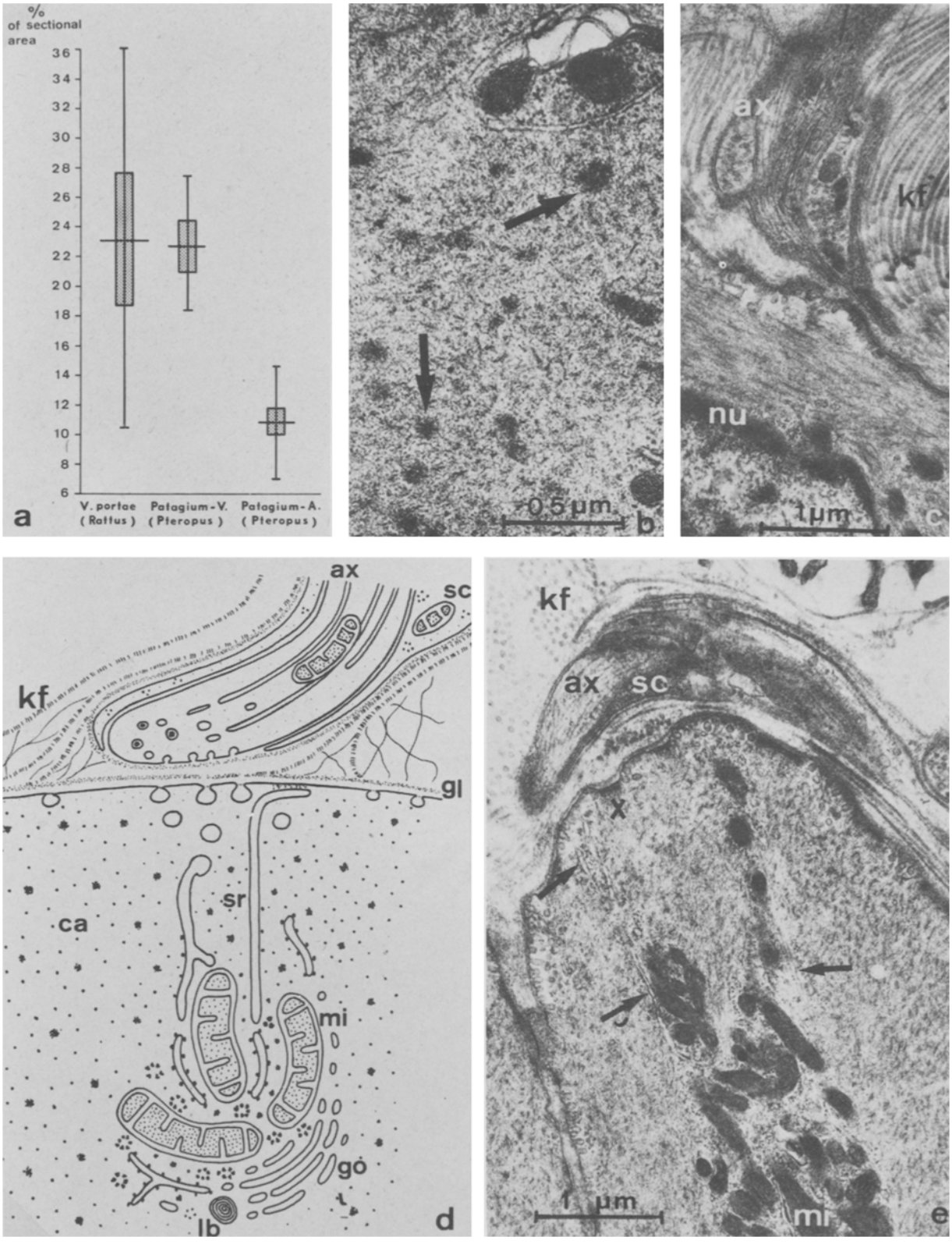

Fig. 2. *a* Diagram of the relative content of sarcosomes in the muscle cells of autonomously contractile veins and a patagium artery; *b* dense patches (arrows) in a cross-sectioned muscle cell of a *Pteropus*-vein; *c–e* neuro-muscular contact area in the peripheral t. media of a vein of *Pteropus*; axon (ax), Schwann cell (sc), collagenous fibre (kf), glycocalix (gl), sarcoplasmic reticulum (sr resp. arrows), sarcosomes (mi), lamellated body (lb), Golgi system (go), hemidesmosome-like structures (x), contractile apparatus (ca), further explanations see in text.

channels of the sarcoplasmatic reticulum very often connect the cell surface with the accumulations of mitochondria of the central area. Such connections are particularly developed in the peripheral muscle cells of the media, that is in the region of neuromuscular synapses (figure 2, c–e). The findings of other authors on vascular smooth muscles[10,12] suggested employing strontium as a tracer to show that the sarcoplasmic reticulum of smooth muscles plays a role similar to that of striated muscles. It functions as a source of activator calcium and a site into which calcium is actively accumulated during relaxation[4,10]. On account of these authors' findings there is every reason to believe that the extensive sarcoplasmic reticulum, especially the straight channels mentioned above, functions as the passage for a fast influx of Ca.

The pharmacochemical trigger mechanism, which activates the contractile apparatus by causing a rise in intracellular free calcium, is realized by the neurotransmitter substances of numerous nerve endings in the contact area of t. adventitia and t. media. These are polyaxonal, nonmyelinated nerves entering jointly with the vasa vasorum into the t. adventitia but not into the inner t. media. Near the synaptic area, the Schwann-cell sheath is partially opened and connected to the glycocalix of processes of the muscle cell by a web of collagenous fibres and reticular filaments, so that a permanent synaptic contact is given (figure 2, c–e), which is independent of the contractile status of the vessel. However, the intersynaptic gap seems to be variable (0.2–1.0 µm). It changes in dependence of the contractions of the muscle cell. This type of a neuromuscular synaptic relation seems to be embodied in nearly all vertebrate vessels investigated so far and has been called 'the synapses at distance'[13]. The terminal axoplasm contains neurotubuli, some few mitochondria, as well as synaptic vesicles of different sizes with and without dense cores. Since special fluorescence microscopical or histochemical results concerning the type of nerve endings in the patagium veins, have been published the granulated vesicles only give an indication of an adrenergic resp. the nerve endings with clear synaptic vesicles to an cholinergic innervation of the muscle cells in the peripheral vessel wall. The central, in general not directly innervated muscle cells of the inner media probably seem to be stimulated by an electrical trigger mechanism beginning in the peripheral, nervously controlled muscle cells[14–16]. The numerous closed interdigitations (figure 1, b) with gap junctions between the muscle cells could be an important prerequisite for such a mechanism.

These very close connections of the muscle cells, the well developed system of sarcoplasmatic reticulum, such as the channel system of Ca^{++}-influx, combined with the high content of electron dense sarcosomes are the most remarkable characteristics of this vessel type, i.e. the ultrastructural substrate of its intrinsic myogenous automaty which has been demonstrated by the in vitro pulsations of the isolated vessel[1–3,14].

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The chemical and pharmacological milieu

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Although the bat can hardly be considered to be universally popular as an experimental laboratory animal compared to rats, cats, dogs or rabbits, there are many important and specific ways in which this highly developed mammal can be used to advance our knowledge.

A list of the advantages of the bat as an experimental animal should include the ease with which the wing vasculature can be observed microscopically and the fact that no anesthesia or surgery is needed for in vivo microscopic observation. The small laboratory space needed for storing the animals and the minimal effort required to maintain them is an advantage. Most importantly, there are many aspects of the cardiovascular system which can be studied encompassing such diverse areas as the architectural structure of the