TROPHOBLAST IN CHIROPTERAN DEVELOPMENT

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ABSTRACT

In bats the trophoblastic layer exhibits distinct polarity which determines the blastocyst-uterus relationship. During advanced stages of development there appears to be regional differentiation of the trophoblast, and this is reflected in the various kinds of placental formations during gestation in these animals.

INTRODUCTION

STUDIES on the embryology of mammals[1] reveal a highly specific topographical relationship between the implanting blastocyst and the maternal uterus. The location and nature of the placenta and associated structures are nearly constant within a given family and, sometimes, within a given order. The trophoblast is, perhaps, the most important structure involved in the events of embryonic life of eutherian mammals since it is mainly responsible for implantation of the blastocyst and establishment of the placenta. Structural differences in the trophoblast in different regions of the free blastocyst have not been established so far. This poses an interesting question: Is there any regional physiological differentiation in the trophoblast at the blastocyst stage and during the later embryonic life? The present paper is an attempt to answer this question and propose a hypothesis that the mammalian embryo has a distinct physiological polarity. This report is based on the examination of gravid uteri carrying embryos at different stages of development of at least one species from each of the nine families of Chiroptera available in India.

MATERIALS AND METHODS

Developmental stages of the following species were studied: (figures in parentheses represent the number of pregnant specimens examined). *Pteropus giganteus giganteus* (78), *Cynopterus sphinx gangeticus* (165) (both Pteropidae), (*Rhinopoma kinneari* (113) (Rhinopomatidae), *Taphozous longimanus* (129) (Emballonuridae), *Rhinolophus rouxi* (285) (Rhinolophidae), *Hipposideros bicolor pallidus* (36), *H. ater ater* (268), *H. speoris* (280) (all Hipposideridae), *Megaderma lyra lyra* (334) (Megadermatidae), *Scotophilus temmincki* (168), *Pipistrellus ceylonicus chrysothrix* (245) (both Vespertilionidae), *Miniopterus schreibersii fuliginosus* (447) (Miniopteridae) and *Tadarida aegyptiaca* (102), *T. plicata* (128) and *T. tragata* (3) (all Molossidae). The specimens were collected during the past 40 years from different parts of India.

Since detailed descriptions of the development of nearly all these species of bats have already been reported, histological details have not been given in this report. However, references to these have been indicated at the relevant places.

OBSERVATIONS

Trophoblast in the blastocyst

The topographical relationship between the blastocyst and the uterus was described earlier[2]. The nature of the attachment and the orientation of the embryonic mass within the uterus vary among the different species, and these are illustrated in figure 1. Three major differences are noticed: (i) Partly interstitial implantation in *Pteropus*[3], (ii) Superficial diffuse implantation in *Cynopterus*[4], *Rhinopoma*[5], *Rhinolophus*[6], all hipposiderid species[5,7,8], *Megaderma*[9], *Miniopterus*[10,11], *Tadarida*[12], and (iii) Superficial localized implantation as in the vespertilionid bats[13]. The location of the embryonic mass is mesometrial or slightly towards the lateral side in *Pteropus*, *Cynopterus*, *Rhinopoma*, *Rhinolophus*, *Hipposideros* and *Taphozous*, variable in *Megaderma* and antimesometrial in *Tadarida*, all vespertilionids and *Miniopterus*.

These variations reflect the differences in the intensity and extensiveness of cytolytic activity of the trophoblast not only in different regions of the blastocyst but also in the blastocysts of different species. Whereas the trophoblast penetrates deep into the uterine endometrium in *Pteropus*, it becomes superficially and circumferentially implanted in all the species except vespertilionids.

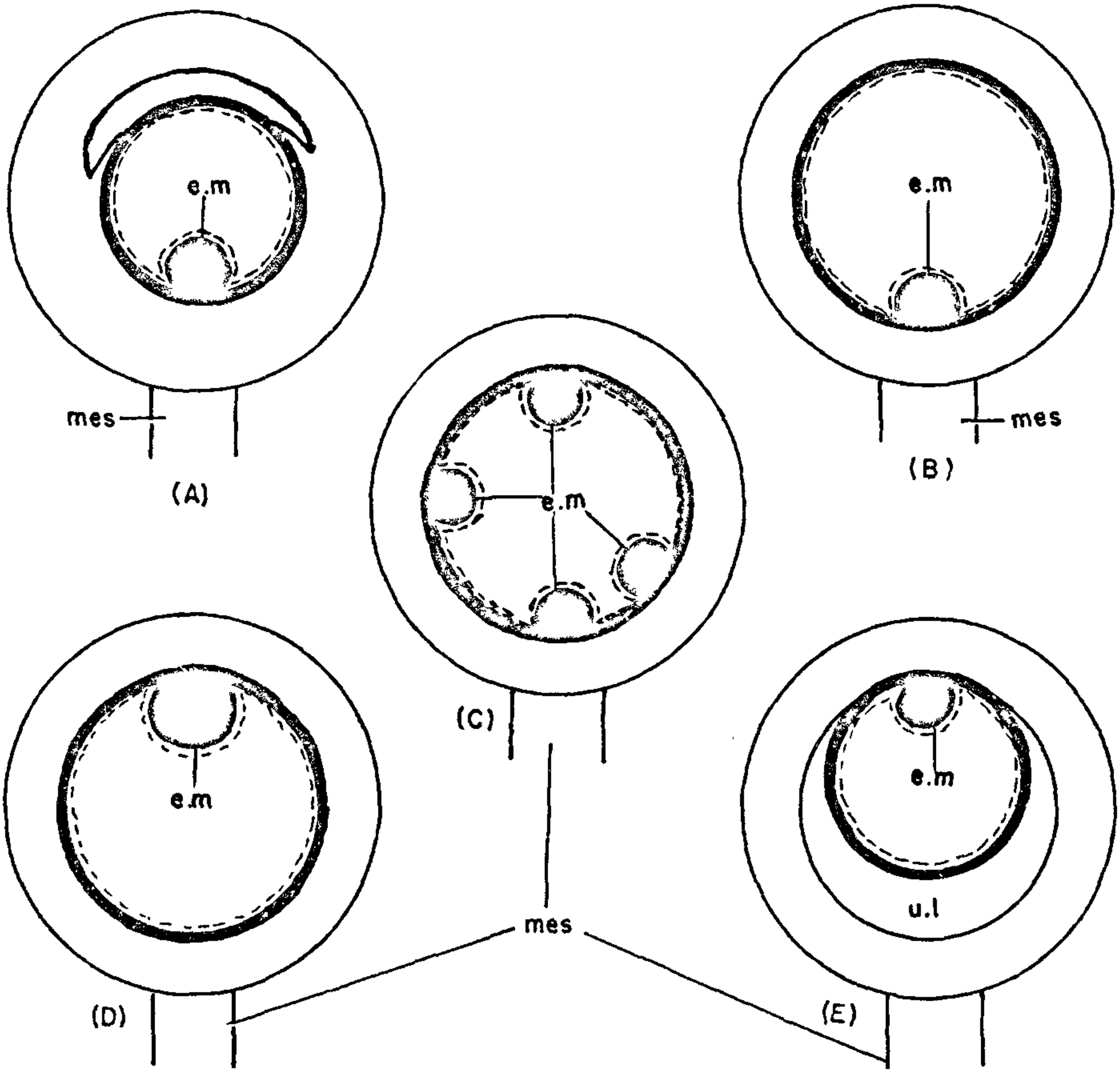

Figure 1. Schematic drawings to illustrate implanted blastocyst. The dark solid line represents trophoblast and the discontinuous line represents extra-embryonic endoderm. (A) *Pteropus*; (B) *Rhinopoma*, *Taphozous*, *Hipposideros*, *Rhinolophus*; (C) *Megaderma* — embryonic mass has variable orientation; (D) *Tadarida*, *Miniopterus*; (E) Vespertilionida. [e.m: embryonic mass; mes: mesometrium; u.l: uterine lumen.]

In vespertilionids the cytolytic action of the trophoblast is confined to the embryonic hemisphere of the blastocyst, the other regions of the blastocyst not even establishing contact with the uterine wall. Further, there appears to be a decreasing physiological gradient in the cytolytic potentiality of the trophoblast from the embryonic to the abembryonic regions if the blastocyst in all the species except *Miniopterus*[11] and *Tadarida*[12]. In these two species the trophoblast penetrates deep into the endometrium on all the sides of the implantation chamber except in the region adjacent to the embryonic mass where the trophoblast destroys only the epithelium, but does not invade the endometrial tissue. Further, as the embryonic mass expands into a plate, the trophoblastic layer overlying the embryonic plate becomes stretched and finally gets torn out.

Post-implantation development

The course of development and the final location and structure of the placenta vary in different species due to differences in the activity of the trophoblast. The various types of relationships between the placenta and the uterus at about late limb-bud stage of development of the foetus are illustrated in

figure 2. These can be recognised into the following four types. (i) Cup-shaped allantoic placenta occupies nearly half of the uterine wall, and smooth chorion occurs in the rest of the gestation sac. This situation occurs in *Pteropus*[3], *Cynopterus*[4], *Rhinopoma*[5], *Rhinolophus*[14], *Hipposideros*[5,15] and *Megaderma*[16]. In all species of these genera the chorion is closely apposed to the superficial surface of the endometrium. In Vespertilionidae the abembryonic part of the chorion lies freely in the uterine lumen[17]. The placenta is mesometrial in all the species except vespertilionids in which it is antimesometrial. (ii) There is a diffuse placenta on all the sides of the gestation sac except on the mesometrial side where there is a discoid placenta. This occurs in *Tadarida*[18]. It is interesting that the discoid placenta is formed on the abembryonic side in this animal. (iii) There are two kinds of placenta, a primary placenta consisting of relatively simple tubules occurring on the antimesometrial side, and two secondary placental discs composed of labyrinthine placental tubules at the cranial and caudal margins of the

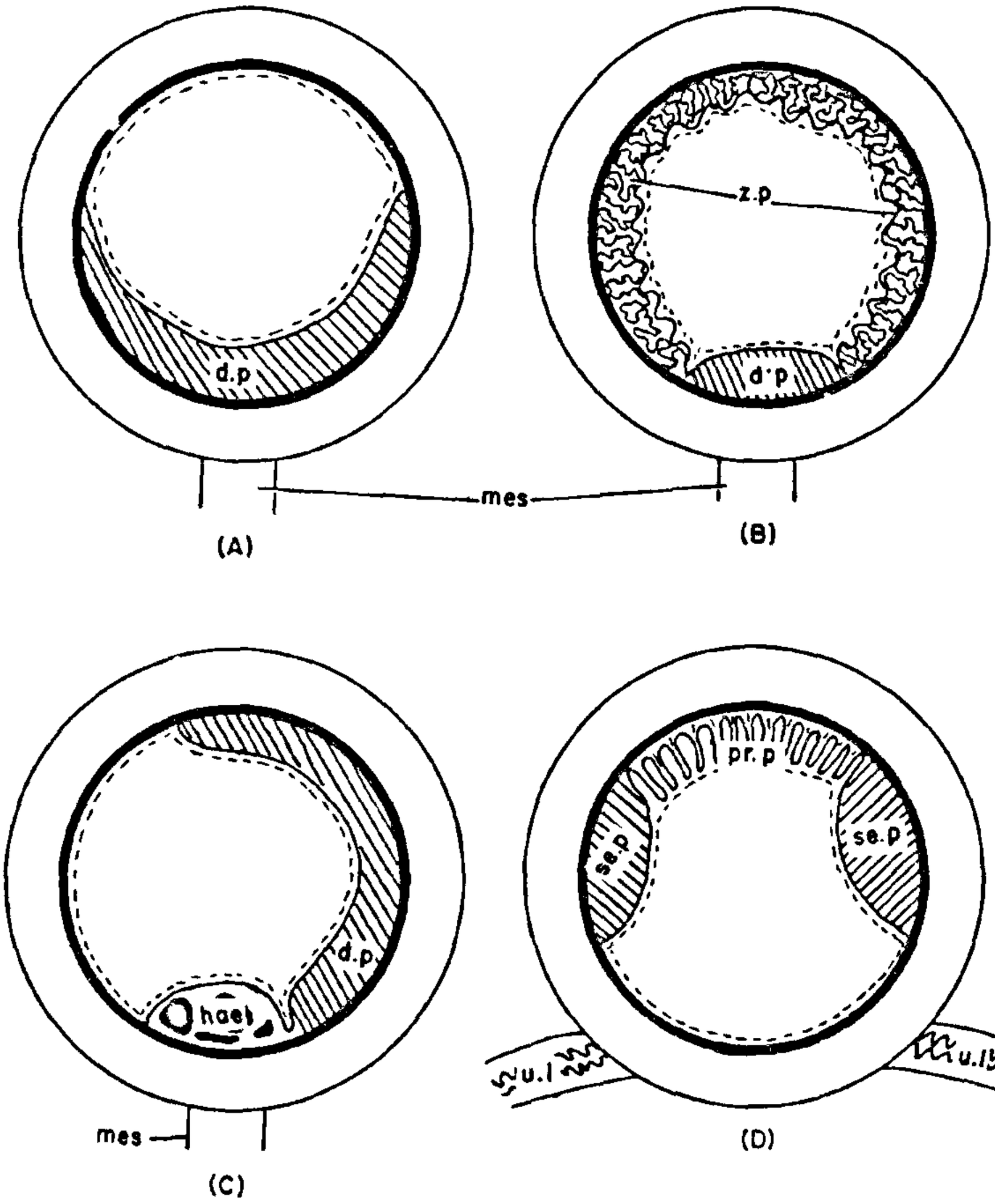

Figure 2. Schematic drawings to illustrate the location of the placenta at late limb-bud stage of development. (A) *Pteropus*, *Rhinopoma*, *Rhinolophus*, *Hipposideros*, *Megaderma*; (B) *Tadarida*; (C) *Taphozous*; (D) *Miniopterus*. [d.p.: placental disc; hae: haematoma; pr.p: primary placenta; se.p: secondary placenta; z.p: zonary placenta. Other legends as in figure 1.]

primary placenta. Smooth chorion is in contact with the superficial region of the endometrium in the rest of the gestation sac. This situation obtains in *Miniopterus*[10]. (iv) The placenta becomes separated by a deep cleft into two parts, a lateral and a mesometrial part as in *Taphozous*[5]. The lateral moiety is a typical labyrinthine placenta. The mesometrial part of the placenta has large maternal blood spaces surrounded by hypertrophied trophoblast cells. This is the beginning of the formation of an haematoma. Figure 3 illustrates the different kinds of placenta and their location in all the bats at full term. The placenta is discoidal and mesometrial in all the species except *Taphozous* and *Miniopterus*. In *Taphozous* the main placenta is lateral and discoid, and a large haematoma occurs on the mesometrial side. In *Miniopterus* the primary placenta is antimesometrial and is in the form of a few simple degenerating tubules embedded in allantoic mesenchyme. A large secondary placental disc occurs on either side of the primary placenta. A tertiary placenta is formed within each secondary placental

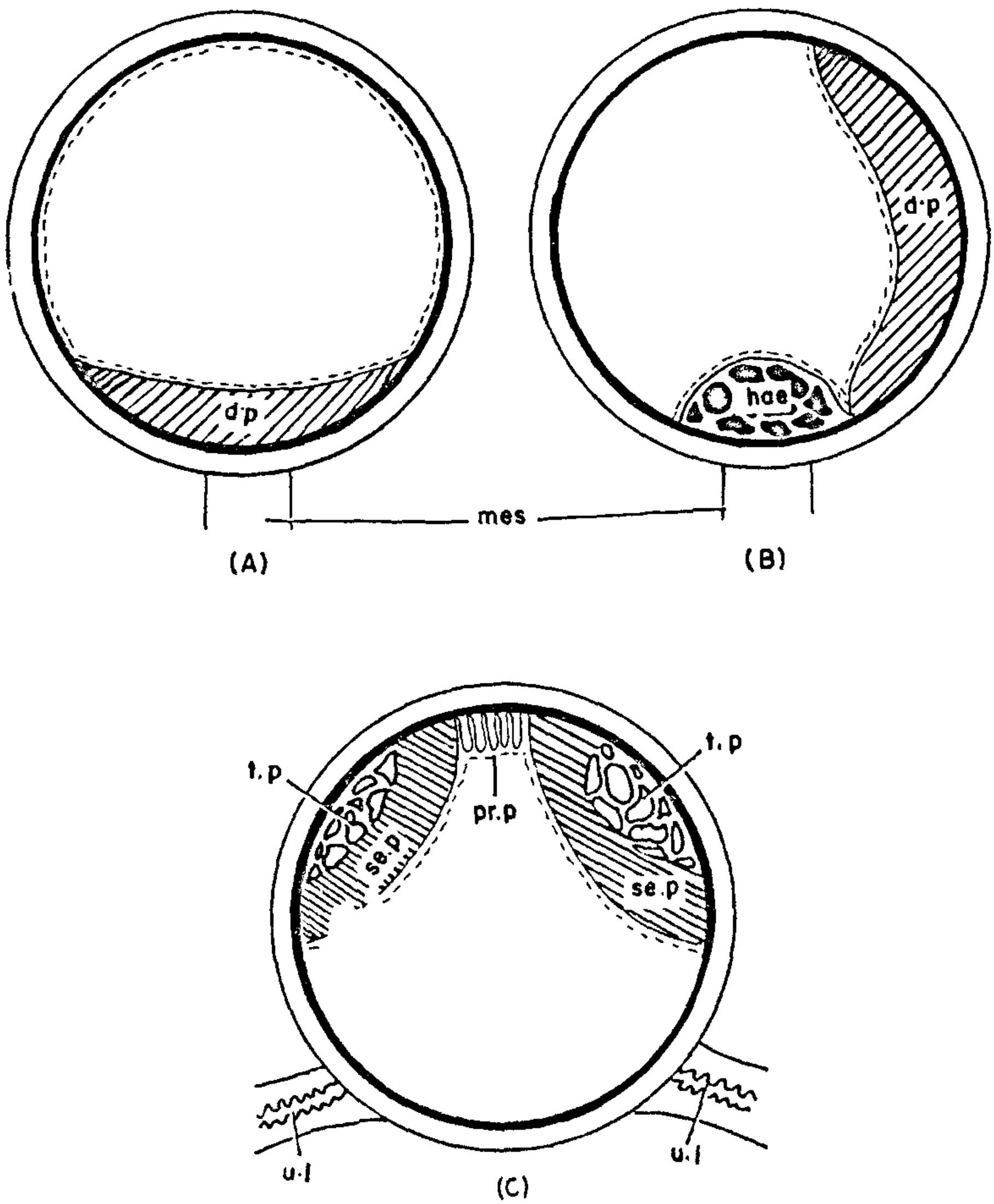

Figure 3. Schematic drawings to illustrate the position of the definitive location of the placenta. (A) *Pteropus*, *Rhinopoma*, *Rhinolophus*, *Hipposideros*, *Megaderma*; (B) *Taphozous*; (C) *Miniopterus*. [t.p: tertiary placenta. Other legends as in figure 1.]

disc near its myometrial border. In vespertilinoids the placenta is discoid and is squarely on the mesometrial side, and the uterine lumen on the mesometrial side is artificially obliterated by the apposition of the chorion to the uterine wall due to the enlargement of the foetus.

DISCUSSION

The foregoing account indicates that in the bats there is a distinct species-specific physiological gradient in the activity of the trophoblast at the blastocyst stage of development and this largely determines the future relationship between the placenta and the uterus. During early development some kind of physiological polarity apppears to determine the topographical relationship between the blastocyst and the uterus. It also seems to determine the pole of the embryo which establishes attachment to the uterine wall and the extent invasion of the trophoblast into the uterine endometrium.

On implantation of the blastocyst, the development of the placenta differs considerably among the different species. Thus, although implantation is difuse in most species (except Vespertilionidae and probably also in *Pteropus*) the final location and structure of the placenta vary among bats. Since histogenesis of the placenta is the function mainly of the trophoblast, it is evident that the characters of the trophoblast differ in different areas in different species. In all bats except in *Tadarida* the trophoblast overlying the embryonic disc produces the final placenta. In *Tadarida* the final placenta is formed by the trophoblast on the abembryonic side. Further, while a part of the trophoblast is active during the early phase embryonic development, a different region of the trophoblast seems to spring into activity after the limb-bud stage of development. This is related to morphological polarity, first during implantation of the blastocyst and then after the invasion of the endometrium by the trophoblast. Almost certainly in *Taphozous*, *Tadarida* and *Miniopterus* the activity of the trophoblast varies in different regions after the limb-bud stage resulting in the formation of different kinds of placenta in different parts of the uterus.

ACKNOWLEDGEMENT

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