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Peculiarities of the formation of the caudiciform part of *Petopentia natalensis* (Schltr.) Bullock (Apocynaceae)

Yaroslav AVIEKIN
Nataliia NUZHYNA
Maryna GAIDARZHY
Kyiv Taras Shevchenko National University,
Educational and Scientific Centre «Institute of Biology and Medicine»,
str. Symona Petlyury, 1, 01032 Kyiv (Ukraine)
avekinyarik@gmail.com
nuzhynan@gmail.com (corresponding author)
gaidarzhy@ukr.net

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ABSTRACT
The anatomical and morphological structure of the seeds and vegetative organs of the endemic caudiciform plant of South Africa *Petopentia natalensis* (Schltr.) Bullock (Apocynaceae) has been investigated at different stages of ontogenesis: seedlings, juvenile and immature plants. It has been noticed that endosperm of *P. natalensis* seeds is developed similar to endosperm of seeds of mesophytic representatives of the Apocynaceae family. Seedling hypocotyl is also of mesophytic type in contrast to those of such succulents as *Adenium obesum* (Forssk.) Roem. & Schult. and *Pachypodium lamerei* Drake. In juvenile plants of *P. natalensis* the hypocotylous zone is constantly increasing to form an enlarged basal part of the stem. Conducting tissues have a different pattern of development in the hypocotyl and epicotyl. In the basal part of the stem they are represented by collateral vascular bundles scattered among the parenchymal cells, while in the climbing part of the stem, the conducting system is represented by a complete ring. Unlike other immature caudiform plants, *P. natalensis* has the bundle type of conducting system. As a rule, the basal expanded part of the *P. natalensis* stem is formed exclusively from the hypocotyl and it occurs mostly due to generation of abundant number of cortical and pith parenchymal cells.

KEY WORDS
Apocynaceae,
South Africa,
anatomy,
seedlings,
juveniles,
immature plants,
hypocotyl,
succulence.

RÉSUMÉ
Particularités de la formation de la partie caudiciforme de Petopentia natalensis *(Schltr.) Bullock (Apocynaceae).*
La structure anatomique et morphologique des graines et des organes végétatifs de la plante caudiciforme, endémique d'Afrique du Sud, *Petopentia natalensis* (Schltr.) Bullock (Apocynaceae) a été étudiée à différents stades de l'ontogenèse : plantules, individus juvéniles et immatures. Il a été constaté que l'albumen des graines de *P. natalensis* se développe comme celui des représentants mésophytes de la famille. L'hypocotyle des plantules est également de type mésophyte, contrairement à celui de succulentes telles que *Adenium obesum* (Forssk.) Roem. & Schult. ou *Pachypodium lamerei* Drake. Dans les individus juvéniles de *P. natalensis* la région hypocotylaire s'accroît constamment pour construire la base élargie de la tige. Les tissus conducteurs suivent un schéma de développement différent dans l'hypocotyle et l'épicotyle. Dans la région basale de la tige, ils sont représentés par des faisceaux phloémo-xylémiens collatéraux, dispersés dans le parenchyme, tandis qu'ils forment un anneau complet dans la région supérieure volubile. Contrairement aux individus immatures d'autres plantes à caudex, *P. natalensis* possède un système conducteur de type fasciculaire. En règle générale, la base élargie de la tige de *P. natalensis* provient exclusivement de l'hypocotyle et résulte essentiellement de la prolifération des cellules parenchymateuses du cortex et de la moelle.

MOTS CLÉS
Apocynaceae,
Afrique du Sud,
anatomie,
plantules,
individus juvéniles,
individus immatures,
hypocotyle,
succulence.

INTRODUCTION

Apocynaceae are characterized by a wide pantropical distribution and various habits. Adaptation to life in a variety of environmental conditions led to the formation of anatomical and morphological features characteristic to this family: complex reproductive organ specialization; formation of intraxylary phloem; presence of excretory tissues in the form of laticifers, resulting in the accumulation of various metabolites throughout the plants. Within the family there is a large number of succulent species represented by various life forms: trees, bushes, shrubs, weeds, as well as leaf, stem, pachycaul and caudiciform succulents (Rowley 1999; Eggli 2002; Albers & Meve 2004; Endress *et al.* 2014).

The term "caudiciform" was proposed by Rowley (1987) for plants in which succulence occurs due to basal modifications of the stem. Caudiciform plants include more than 20 taxa of the following families: Asparagaceae Juss., Dioscoreaceae R.Br., Cucurbitaceae Juss., Euphorbiaceae Juss., Vitaceae Juss., Malvaceae Juss., Passifloraceae Juss. ex Roussel and Apocynaceae Juss. The following terms are also used to describe the morphological characteristics of such plants: "bulb", "grotesque expanded base", "caudex". For example, *Pachypodium succulentum* (L. f.) Sweet is described in the literature as having a "caudex", and *P. rosulatum* Baker – a plant with a "massive trunk"; *Cyphostemma bainesii* (Hook. f.) Descoings – as "pachycaul plant, with a globose trunk", while morphologically similar *C. juttae* (Gilg & Brandt) Descoings and *Kedrostis africana* (L.) Cogniaux – as plants with a "tuberous caudex"; and *Ficus palmeri* – as "caudiciform plant" (Rowley 1987; Eggli 2002; Albers & Meve 2004). This suggests a lack of structural and developmental information about these modifications, which could determine the biomorphological status of these plants in more details (Pate & Dixon 1982; Eggli & Nyffeler 2009).

Based on anatomical and morphological studies conducted on adult caudiciform plants of the genus *Adenia* Forssk. (Passifloraceae), it was established that many taxa of this genus exhibit a significant expansion of the basal part of the stem and, partially, of the root. Almost all studied taxa are characterized by a noticeable primary thickening due to the growth of the pith and cortical parenchyma. Parenchymal thin-walled cells were marked by their large size, high content of starch grains and lipids. A distinctive pattern of developed specialized wood was found, which, like in some pachycaul plants (*Adansonia* L., *Cyphostemma* (Planchon) Alston, *Dorstenia* L.), was marked by significant parenchymatization (Fisher 1981; Hearn 2006, 2009, 2013; Wickens & Lowe 2008; Kotina *et al.* 2017). As a result of comparisons of the biomorphological and structural features, it was hypothesized that caudiciform and pachycaul succulents are closely related to the mesophytic representatives (Olson 2003; Hearn *et al.* 2018). So, Olson (2003) noted that the evolution of pachycauls from lianas had happened repeatedly. On the other hand, the hypothese that root succulent plant species are more closely related to stem succulent plant species than expected by chance, was statistically supported by Hearn *et al.* (2013), who suggest tuberous roots may foreshadow stem succulence. But these assumptions cannot be fully analyzed due to the lack of detailed information on the anatomy and morphology of caudiciform plants from different taxa and at different, especially early, development stages, preventing a complete understanding of the appearance of certain modifications, from which parts of the shoots and due to which tissues.Our studies focused on the anatomical and morphological structure of the seeds and vegetative organs of the endemic caudiciform plant of South Africa *Petopentia natalensis* (Schltr.) Bullock (Apocynaceae, Asclepiadoideae) at different stages of ontogenesis: seedlings, juvenile and immature plants.

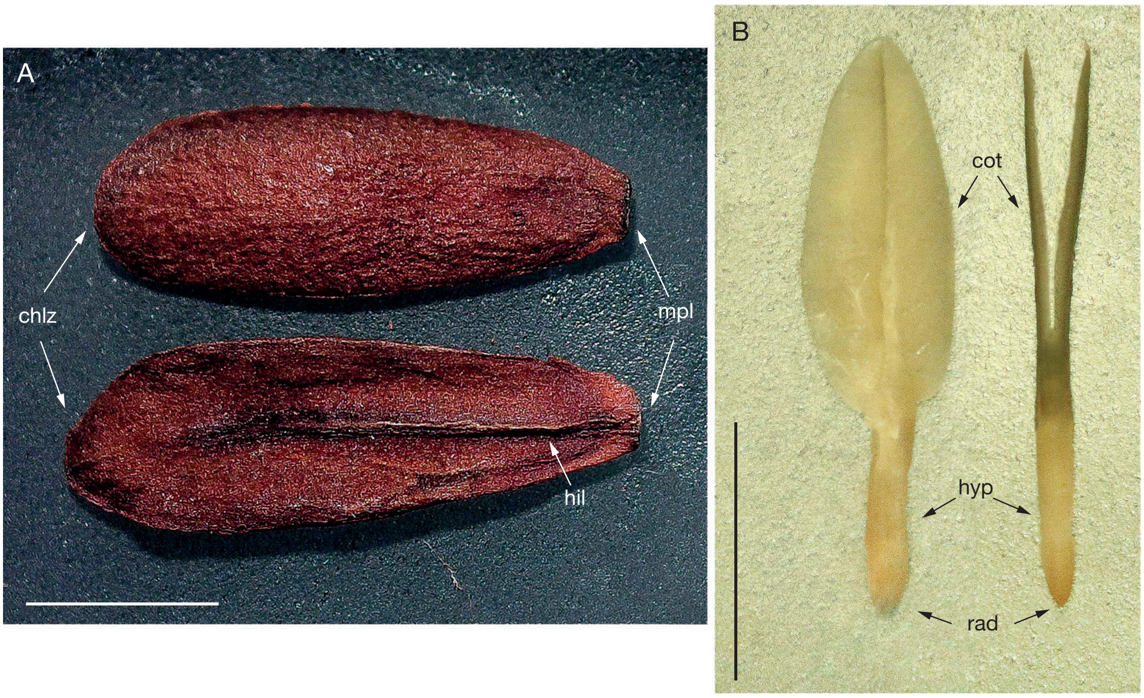

Fig. 1. — Morphological features of seeds and embryo of *Petopentia natalensis* (Schltr.) Bullock: **A**, general view of seeds without pappus from the dorsal and ventral sides; B, general view of the embryos from the dorsal and lateral sides in the longitudinal section. Abbreviations: **chz**, chalaza; **hil**, hilum; **mpl**, micropyle; **cot**, cotyledons; **hyp**, hypocotyl; **rad**, radicle. Scale bars: 5 mm.

MATERIAL AND METHODS

The representative of the endemic, monotypic genus *Petopentia* Bullock is *Petopentia natalensis*, growing in the semi-arid savanna forest of the KwaZulu-Natal province in South Africa. It is a vine having more or less rounded tuber, up to 40 cm in diameter, which may be partially immersed in the soil. The surface of the tuber is covered with a reddish-brown bark and has small longitudinal cracks. Lianoid shoots may reach 15 m in length and 0.3-0.5 cm in diameter. During rain-free periods, the herbaceous part of the shoots dies off. The leaves are simple, linear, from 5 to 13 cm long and 1-6 cm wide, on short petioles, opposite, leathery, glossy dark green from the adaxial side and violet from the abaxial side. Flowers are 5-merous, combined in small inflorescences, formed from the axillary buds on the vine. The fruits are represented by double, flattened spindle-like follicles of greenish-brown color (Albers & Meve 2004).

The research was carried out based on the collection of succulent plants of the Botanical Garden named after academician O.V. Fomin of the Kyiv National Taras Shevchenko University. Plants were grown from seeds. The sample for each stage was 10. When characterizing ontogenesis, the method described by Vasiliiev *et al.* (1978) and Zhmilyov *et al.* (2005) was used, which distinguishes several periods: latent (mature seed); virgin or pregenerative, which is divided into three stages - seedling, juvenile (with cotyledons and small leaves) and immature (no cotyledons and with formed leaves) plant; as well as generative and senile periods.

The morphological structure of the seeds was described by Takhtajyan (2010). Seeds and vegetative parts of plants were fixed in FAA, embedded in gelatin according to the Romeis method (1948), and sectioned on a freezing microtome. The slices were stained with 1% safranin in 50% ethanol for 5 minutes (Romeis 1948). Microscopic measurements were performed using an Olympus System Microscope Model BX 41 (Tokyo, Japan) and Image J program. The Statistica 8 program was used for statistical data processing. The values for different groups were compared by the t-test.

Abbreviation

BPS Basal part of the stem.

RESULTS

Latent period, seed

Seeds of *P. natalensis* are of the anatropous type, bilaterally flattened, elongated, obovate, or almost elliptical 14.8 ± 0.7 mm long, 5.7 ± 0.5 mm wide and 1.4 ± 0.2 mm thick. The surface of the seed is smooth brown with a few folds. In the central area of the dorsal side of the seed there is a clearly defined long hilum, which occupies ¾ of its length (Fig. 1A). In the zone of the micropyle is an anemochorous adaptation, consisting of bundles of numerous trichomes of 30±3.5 mm long.

The embryo occupies a central position in the seed and is completely surrounded by endosperm. The cotyledons are

Table 1. — Morphometric indices of tissues in plants of *Petopentia natalensis* (Schltr.) Bullock at different stages of ontogenesis. Abbreviation and symbol: **BPS**, basal part of the stem in juvenile and immature plants; *****, P ≤ 0.05, comparative to the previous stage of ontogenesis.

			Tissue thickness, µm (M±SD)		
Organs	**Tissues**		**Seedlings**	**Juvenile plants**	**Immature plants**
Upper part of the stem	Epidermis		–	20.2±2.9	–
	Periderm	Phellem	–	65.6±11.7	127.4±35.7*
		Phelloderm	–	42.3±7.2	79.8±11.3*
	Cortical parenchyma		–	90.2±18.5	165.3±39.6*
	Phloem		–	54.1±7.8	93.7±31.3*
	Xylem		–	128.5±28.4	163.6±45.6*
	Pith		–	119 ± 35.1	165.6 ± 24.3*
Hypocotyl / BPS	Epidermis		19.7±2.8	21.5±3.1	–
	Periderm	Phellem	–	98.7±13.9	255.2±62.8*
		Phelloderm	–	74.2±11.5	109.8±28.4*
	Cortical parenchyma		216.2 ± 41.1	631.4±112.7*	2284.7±295.9*
	Protophloem / Phloem		30.5±7.6/	/98.4±13.5*	/216.1±34.2*
	Protoxylem / Xylem		55.7±14.3/	/134.2±38.7*	/462.6±73.5*
	Pith		238.6 ± 57.2	727.3 ± 132.1*	14476 ± 911*
Main root	Epiblema		36.1 ± 9.8	42.1 ± 10.3	–
	Exoderm		57.2 ± 21.1	68.5 ± 19.2	–
	Periderm	Phellem	–	–	176.8±32.2
		Phelloderm	–	–	82.6±17.9
	Cortical parenchyma		144.6±45.1	153.5±52.6	246.4±62.3*
	Protophloem / Phloem		29.5±8.4/	/57.2±16.7*	/59 ± 14.1
	Protoxylem / Xylem		36.3±11.1/	/88.1±20.2	/438.1 ± 182.5*

elongated elliptical, 4.2 ± 0.3 mm long, 1.4 ± 0.2mm wide and 0.8 ± 0.1 mm thick, they occupy about 60% of the total volume of embryo. The hypocotyl is narrow and cylindrical 4.4 ± 0.2 mm long and 0.7 ± 0.1 mm in diameter, it occupies about 38% of the volume of embryo. The radicle is represented by a meristematic cone of growth (0.2 ± 0.1mm long and 0.3 ± 0.2 mm in diameter), and it occupies up to 2% of the volume of embryo (Fig. 1B).

Virginal period, seedlings

Seeds of *P. natalensis* germinate 7-8 days after sowing, and complete release from the seed cover. Cotyledon spreading occurs at day 16-19. Lanceolate cotyledons are slightly thickened, hypostomatic, light green from the adaxial and light pink from the abaxial side (Fig. 1B).

Hypocotyl

The hypocotyl is elongated, cylindrical, reddish brown and thin. On cross section of the middle part there is an obvious epidermal layer consisting of cylindrical or cubic cells with thickened lignified walls. Cortical parenchyma is built by 12-16 layers of large, thin-walled isodiametric cells; whose protoplasts contain starch granules. Among the cells of the cortical parenchyma, adjacent to the fiber vascular bundles, occur non-articulated milk vessels with thickened walls. The conducting system of *P. natalensis* seedlings includes 14-18 vascular bundles. Protophloem is thinner than protoxylem. Procambium consists of one layer of small, thin-walled isodiametric cells. The pith is less developed as compared to the cortical parenchyma, composed along the diameter of 5-7 layers of large, thin-walled isodiametric vacuolated cells (Fig. 2A).

Main root

The main root in seedlings of *P. natalensis* is yellowish and exhibits in cross section a 1-layered epiblema, consisting of elongated cylindrical cells with developed root hairs 157.6 ± 46.8 µm in length. The exoderm includes one layer of large cubical or cylindrical cells with thickened walls. Parenchyma of the root cortex is represented by 6-7 layers of isodiametric thin-walled cells, among which there are single non-articulated milk vessels. The central cylinder is represented by well differentiated vessels of protoxylem, surrounded by an almost complete ring of protophloem (Fig. 2B).

Virginal period, juvenile plants

P. natalensis plants have cotyledons and 3-4 pairs of leaves in 60-65 days. Leaves are hypostomatic without expressed succulent traits. At this stage of development, the stem of the juvenile plant can be divided into two parts – upper and lower (basal) ones.

Upper part of the stem

The upper part of the stem is thin, lianoid, orthotropic and characterized by positive heliotropism. The surface of the stem is greenish-brown, the distance between the nodes is 29.7 ± 6.8 mm. On cross section there is an epidermis layer consisting of horizontally arranged cylindrical cells with lignified walls. Under it there is a periderm, built by the two-layered phellem with thick-walled cubic cells, and the two-layered phelloderm, whose cells are thin-walled and cylindrical. Chloroplasts are present in phelloderm cells. The cortical parenchyma contains 3-4 layers of thin-walled isodiametric cells. Non-articulated milk vessels are scattered inside it. Xylem is represented by

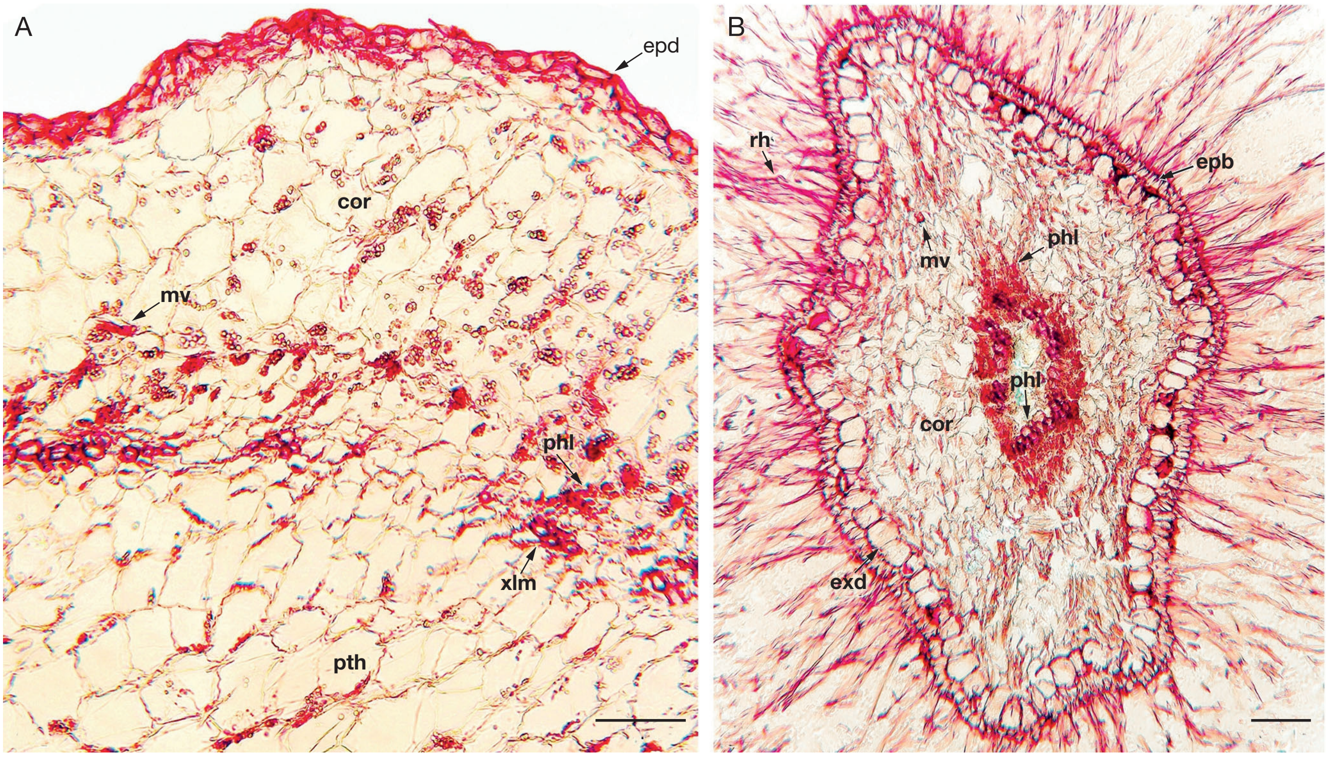

Fig. 2. — Anatomical structure of seedlings (3 weeks) of *Petopentia natalensis* (Schltr.) Bullock: **A**, hypocotyl; **B**, main root. Abbrviations: **epd**, epidermis; **cor**, cortical parenchyma; **phl**, phloem; **xlm**, xylem; **pth**, pith; **mv**, milk vessels; **epb**, epiblema; **exd**, exoderma; **rh**, root hairs. Scale bars: 100 µm.

a complete ring consisting of 4-5 rows of radially arranged vessels. We have noted the formation of additional internal phloem (Fig. 3C[iphl.]). The pith consists of about 5-7 layers of thin-walled isodiametric cells, between which there are a large number of non-articulated milk vessels with thickened walls (Fig. 3A; Table 1).

Basal part of the stem

The basal part of the stem (here in after referred to as BPS) of juvenile *P. natalensis* plants that was derived from hypocotyl is more expanded as compared to its upper part and is clearly determined. The BPS is elongated and fusiform due to its uneven thickening. In the middle part of the BPS, the diameter of the BPS is almost sixfold larger than that near the cotyledons and in the zone bordering the main root.

At this stage, the exfoliation of the epidermis begins. A periderm, consisting of three layers of phellem and three layers of phelloderm, appears. Cortical parenchyma thickens considerably and includes 10-14 layers of large isodiametric thin-walled cells, in which starch grains occur. Within the mass of cortical parenchyma cells there are milk vessels, denser when approaching phloem vessels.

The conducting system retains its collateral bundle structure, the number of vascular fibers of the BPS of juvenile plants is similar to that in the hypocotyl zone of seedlings. Due to the appearance of cambium and the formation of secondary xylem and phloem, bundles are considerably enlarged (Fig. 3C; Table 1). The number of xylem vessels per bundle can range from 12 to 45. The phloem is less developed than the xylem, but zones of additional phloem, 47.1 ± 10.3 µm thick, are formed on the inner side of the xylem along the pith. Together with the increase in number of fiber vascular bundles, the distance between them also grows due to the considerable expansion of the pith rays. The pith, like the cortical parenchyma, thickens almost threefold, as compared with seedlings (Table 1). In this case, not only the number of thin-walled isodiametric cells increases, but their size as well (Table 2). Single milk vessels are also found inside the pith, but their number is significantly smaller as compared to the cortical parenchyma.

Root

In juvenile *P. natalensis* plants, root system was developed and branched significantly as compared to seedlings. In this context, the main root diameter increases slightly, while the length is increased nearly fourfold (Table 3; Figs 4; 5). Up to 10 lateral, yellowish roots are developing additionally, 19.3 ± 8.1 mm long and 0.6 ± 0.2 mm in diameter. The cross section of the middle part of the main root, shows how its secondary structure is initiated. The epiblema layer begins to peel off. Exoderm cells of juvenile plants, as compared to those of seedlings, increase in size, and their walls thicken. Parenchyma of the root cortical is composed of rounded, thin-walled cells, among which there are single milk vessels. The thickness of xylem is twice that in seedlings, which is arranged in a ring-like manner. Thickening results both from an increase in the number of vessels layers (4-5) and their slight enlargement in diameter. Phloem thickness is approximately doubled (Fig. 3B; Table 1).

TABLE 2. — Morphometric indices of cells in plants of *Petopentia natalensis* (Schltr.) Bullock at different stages of ontogenesis (M±SD). Abbreviation and symbol: **BPS**, basal part of the stem in juvenile and immature plants; *****, P ≤ 0.05, comparative to the previous stage of ontogenesis.

Organs	Tissues		Parameters (µm)	Seedlings	Juvenile plants	Immature plants
Upper part of the stem	Epidermis		width	–	21.2±1.5	–
	Periderm	Phellem	width	–	49.2±4.7	52.3±5.1*
		Phelloderm	width	–	32.8±3.7	33.5 ± 4.6
	Cortical parenchyma width		27.3±3.9	34.4±4.7*	–	–
	Pith		diameter	–	50.8±12.4	102.3±53.7*
Hypocotyl / BPS	Epidermis		width	19.5±1.7	24.6±2.4	–
	Periderm	Phellem	width	–	55.8±4.2	61.2±5.7*
		Phelloderm	width	–	46.1±4.6	52.1±5.1*
	Cortical parenchyma width	78.6±14.7	82.1±23.2	112.3±29.5*	–	–
	Pith		diameter	98.5±31.7	131 ±49.6	145.6±52.9
Main root	Epiblema		width	8.3±1.1	6.7±2.3	–
	Exoderm		width	48.2±5.2	54.5±6.2*	–
	Periderm	Phellem	width	–	–	59.1±8.4
		Phelloderm	width	–	–	29.5±5.3
	Cortical parenchyma		diameter	38.8±5.1	45.8±6.7*	81.5±19.4*

VIRGINAL PERIOD, IMMATURE PLANTS

Climbing stem

The length of the climbing stem increases more than fourfold with a slight increase in diameter (Table 3; Figs 4; 5). The lower part of a stem is lignified and strengthened. The surface of the lignified part is rough, red-brown, while in its younger part it is smooth, green-brown. The number of pairs of leaves is 8-9. The average distance between the nodes doubled and is 43.7 ± 14.5 mm. Due to circular nutation to the right, the herbaceous part of a climbing stem twists around the closely located objects and fixes itself in space. At the end of the growing season, the first short internode is lignified, and the other two die. Thus, the climbing stem in the immature representatives of *P. natalensis* is divided into perennial and annual parts (Fig. 5C).

Periderm of the perennial part is twice thicker than in stem of juvenile plants (Table 1). This is due to an increase both in the size of cells and in layer numbers of phellem and phelloderm to 3-4 (Fig. 6A; Table 2). The thickness of cortical parenchyma that consists of 7-9 layers is almost doubled. Conducting tissues are noticeably developing and the thickness of xylem and phloem has approximately doubled. The thickness of the internal phloem is 31.7 ± 10.4 µm. The amount and sclerification of fibers encircling the phloem in a uniform ring increase. In some areas of the stem, the number of fibers increases; they are associated in groups of up to 15 fibers. The pith thickens due to an increase in cell number. Within the mass of pith cells, closer to the internal phloem, there are milk vessels similar to those that are in the cortical parenchyma (Fig. 6A).

Basal part of the stem

The BPS in the immature plants of *P. natalensis* widens in comparison with juvenile plants. Approximately ¼ of the BPS is subterranean and overgrown with adventitious roots 19.4 ± 10.8 mm in length and 0.6 ± 0.1 mm in diameter. The spindle-shaped BPS is changed to a pear-shaped one. There is a clear demarcation near the first node between the succulent expanded BPS, stemming from hypocotyl part of the seedling, and the non-succulent, climbing part of the stem, formed from seedling epicotyl. Periderm of the BPS of immature plants enlarges almost threefold as compared to juvenile plants. This is due to an increase in layer number of phellem to 6-8. The parenchyma of the cortex thickens almost fourfold in comparison with juvenile plants, the size of thin-walled cells increases. Conducting tissues of the BPS maintain their bundle structure. The number of vessels in xylem bundles of the BPS in immature plants is increased to 40-50, as well as the distance between the vascular bundles caused by the intense thickening of surrounding parenchyma. As a result, a part of fiber vascular bundles in the BPS of immature plants is deepened into the pith. The phloem develops less intensively and thickens nearly twofold. Measurements of zones of additional phloem of immature plants do not differ from the juvenile representatives. The pith is intensively developing, and its diameter exceeds more than twenty times the diameter of the pith of juvenile plants. Pith cells are isodiametric, thin-walled, and larger in size than those of the pith cells of juvenile plants (Table 2). The whole BPS is permeated by non-articulated milk vessels (Fig. 6C).

Root

The root system of immature plants *P. natalensis* is characterized by the formation of a large number of lateral roots 32.7 ± 19.2 mm in length and 0.8 ± 0.3 mm in diameter. The length of the main root increases approximately four-

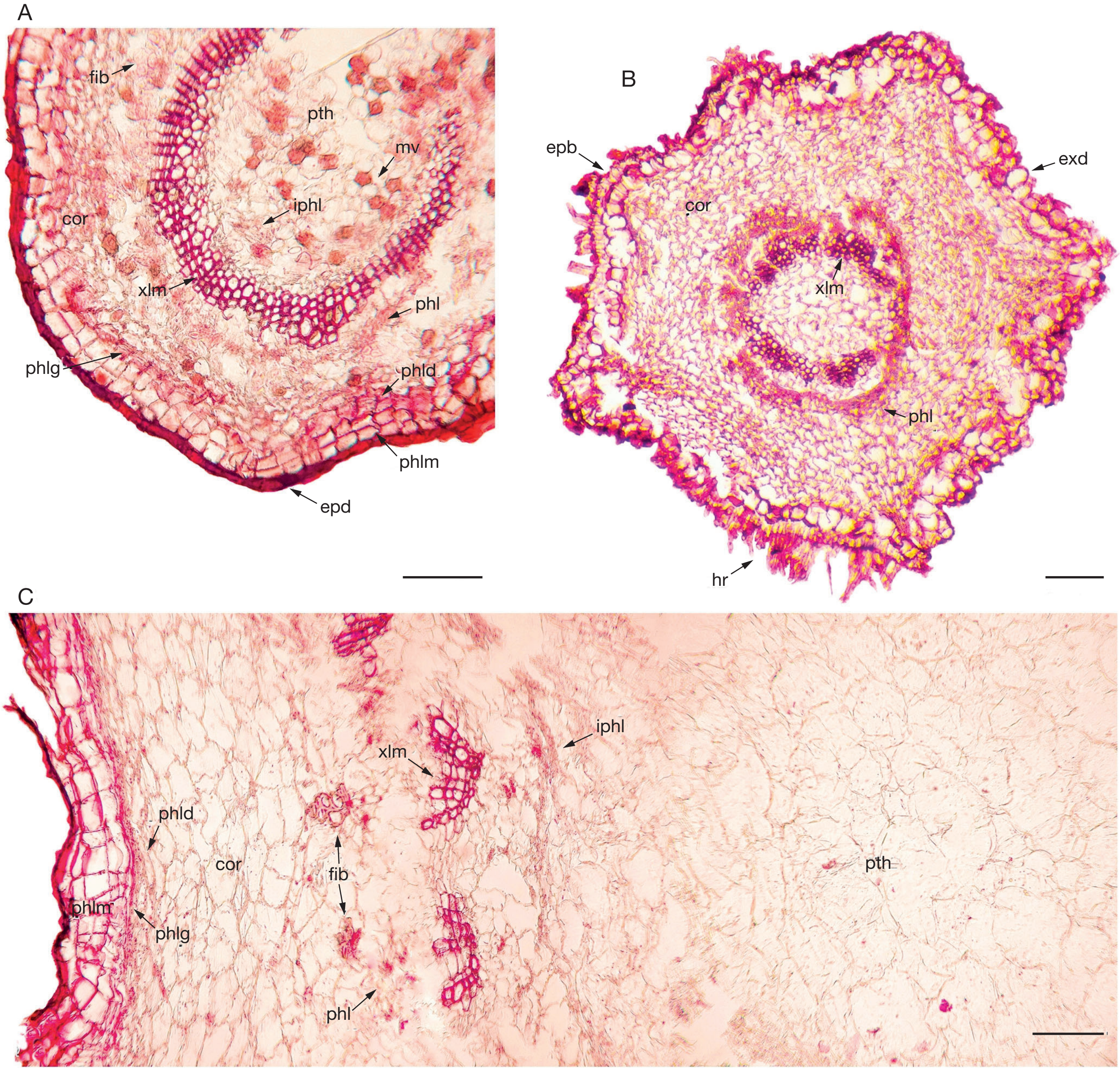

Fig. 3. — Anatomical structure of juvenile plants (8 weeks) of *Petopentia natalensis* (Schltr.) Bullock: **A**, apical part of stem; **B**, main root; **C**, basal part of stem. Abbreviations: **epd**, epidermis; **phlm**, phellem; **phld**, phelloderm; **fib**, sclerenchyma of phloem; **cor**, cortical parenchyma; **phl**, phloem; **xlm**, xylem; **pth**, pith; **iphl**, internal phloem; **mv**, milk vessels; **epb**, epiblema; **exd**, exoderm; **hr**, root hairs. Scale bars: 200 μm.

fold, and the diameter is doubled as compared to juvenile plants. The periderm region of the middle part of the main root is represented by a 3-4-layered phellem, the phelloderm cells are arranged in 3-4 layers. Parenchyma of the cortex includes 5-6 layers of thin-walled isodiametric cells, among which are single, non-articulated milk vessels. The thickness of xylem is fivefold than in juvenile plants. Especially, xylem thickens resulting in a polyarchal star. Vessels of xylem are arranged in strands of 25-30 vessels. The phloem is considerably thinner than the xylem (Fig. 6B; Table 1).

DISCUSSION

The embryo of *P. natalensis* is typical for most representatives of the Apocynaceae family in which the cotyledons exceed in size the hypocotyl. The endosperm in *P. natalensis* seed is much more distinctive than in *Adenium obesum* (Forssk.) Roem. & Schult., *Pachypodium rutenbergianum* Vatke or *Pachypodium lamerei* Drake, previously studied by us (Aviekin *et al.* 2016). Nutrients accumulate not in the hypocotyl, but in well developed cotyledons and a plentiful endosperm, typical of mesophytic representatives of

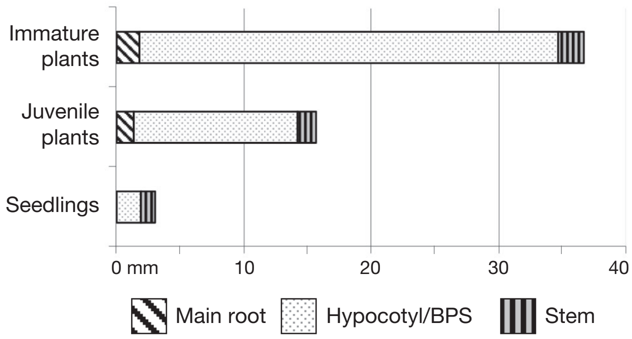

FIG. 4. — Development dynamics of vegetative organs *Petopentia natalensis* (Schltr.) Bullock at different ontogenetical stages (diameter). Abbreviation: **BPS**, basal part of the stem in juvenile and immature plants.

TABLE 3. — Morphometrical indices of plants *Petopentia natalensis* (Schltr.) Bullock at different ontogenesis stages (M±SD). Abbreviations: **l**, length; **w**, width; **s**, thickness; **BPS**, basal part of the stem in juvenile and immature plants.

Organs		Seedlings	Juvenile plants	Immature plants
Cotyledons/ leaves	l (mm) w (mm) s (mm)	6.3±1.3/ 2.1±0.4/ 0.4±0.1/	/46.2±9.8 /16.4±4.2 /0.4±0.2	/113.2±25.4 /36.7±5.5 /0.5±0.2
Upper part of the stem	l (mm)	–	93.1±21.5	387.2±96.7
Hypocotyl/ BPS	l (mm)	16.5±2.2/	/51.2±6.1	/76.4±9.7
Main root	l (mm)	6.2±1.3	31.9±11.2	112.7±31.8

TABLE 4. — The main differences in the formation of caudiciform part in *Petopentia natalensis* and *Adenium obesum* (Forssk.) Roem. & Schult. (Aviekin *et al.* 2016; Aviekin & Gaidarzhy 2017).

Sign	*P. natalensis*	*A. obesum*
Diameter of embryo hypocotyl	0.7 ± 0.1 mm	2.3±0.5 mm
Diameter of seedling hypocotyl	1.9±0.3 mm	5.5±1.7 mm
Upper part of the stem in the juvenile period	Non succulent Complete ring of fibers	Semi-succulent Individual bundles
BPS of immature plants	Individual bundles	Complete ring of fibers
Caudiciform part	From hypocotyl	From hypocotyl, root and to lesser extent epicotyl

the *Apocynaceae* family (Periasamy 1963; Takhtajyan 2010; Aviekin *et al.* 2016).

We hypothesize that there are two ways in Apocynaceae adaptation to arid conditions. The first way distinguishes *A. obesum* and *P. lamerei*; their embryo shows a thickened hypocotyl with a certain reserve of nutrients giving them an advantage for survival in xeric conditions (Aviekin *et al.* 2016). The seeds of *P. natalensis*, enclosing cotyledon and endosperm reserves, exemplify the second way, and can probably grow only in more humid conditions.

Seedlings of *P. natalensis* do not exhibit any significant succulent trait and are morphologically similar to most of the seedlings of the mesophytic representatives of the family Apocynaceae (Takhtajyan 2010). Comparing *P. natalensis* to *A. obesum* (Aviekin & Gaidarzhy 2017), it can be noted that the hypocotyl of *A. obesum* is continuously thickening, while the active development of the *P. natalensis* hypocotyl begins about at the second week after sprouting. The form of hypocotyl is unique to each species, but their development as a whole follows a similar anatomical process. Due to the presence of chloroplasts in the surface layers of the cortical parenchyma cells, seedling hypocotyls carry out photosynthesis along with cotyledons. The root system also has a similar structure as in *A. obesum*.

Closer to the juvenile period, the BPS of *P. natalensis* noticeably thickens compared with other organs. Its thickening occurs within hypocotyl and is characterized by its unevenness, resulting in a spindle-like BPS. In parallel with the formation of BPS in juvenile plants, an upper part of the stem is formed that carries non-succulent leaves and is morphologically very different from the basal part (Fig. 5). The juvenile leaves of the studied taxon and of *A. obesum* (by all signs, except for size and shape) are similar to cotyledons. Both *P. natalensis* and *A. obesum* can lose the leaves in the dry period. The presence of chloroplasts in the outer layers of the cortex parenchyma, as well as in the cells of the phellem, enables photosynthesis of all aboveground part of the shoots, regardless of the presence of leaves (Carlquist 1980; Chapotin *et al.* 2003; Kotina *et al.* 2017). In *P. natalensis*, the upper part of the stem is thin and non-succulent, whereas in *A. obesum* the upper part of the stem is rather succulent or semi-succulent, due to primary thickening, but much less pronounced compared to the BPS (Aviekin & Gaidarzhy 2017). It should be noted that a periderm is formed in the upper part of the stem and the BPS as soon as the juvenile development stage, which further protects the succulent part of the stem from damage and excessive water loss.

Primary thickening of the BPS in *P. natalensis* occurs due to the growth of the parenchyma of the pith and cortex, while in both the main root and the upper part of the lianoid stem, these tissues hardly develop. Special attention is paid to conducting tissues, as they have different character of development in different parts of juvenile plants (Fig. 5). In the BPS they are represented by collateral vascular bundles scattered among parenchymal cells, showing a slight secondary thickening due to the cambium activity, while in the climbing part of the stem, they are ordered in a complete ring. Supportive tissue develops into a ring of sclerenchymal fibers stemming from protophloem. Fibers also occur in the BPS, but are not represented by a complete ring. Additional zones of inner phloem form in the climbing part of the stem and the BPS. The main root of juvenile plants retains its original structure. The rod-type root system is actively developing and branching, but does not exhibit peculiar modifications. Unlike *P. natalensis,* during the juvenile stage of development in *A. obesum*, the upper part of the stem still retains bundles of conducting elements, but there is already

Fig. 5. — *Petopentia natalensis* (Schltr.) Bullock at different ontogenesis stages: **A**, seedlings; **B**, juvenile plants; **C**, immature plants. Abbreviations: **cot**, cotyledons; **hyp**, hypocotyl; **mr**, main root; **aps**, apical part of the stem; **bps**, basal part of the stem. Scale bars: A, B, 2 cm; C, 5 cm.

an active interfascicular cambium leading to differentiate conducting elements of xylem between the bundles, which are subsequently closed almost in a complete ring (Aviekin & Gaidarzhy 2017).

The most notable changes are observed in immature plants of *P. natalensis*, as they acquire almost all the traits of adult plants. There is an increase in size, and a change in the shape of the leaves, and in the growth of the upper and lower parts of the stem. There is a thickening of the periderm, which covers the lower part of the climbing stem, the BPS and the main root. The main root lengthens actively and deepens into the soil, firmly fixing the plant while forming a branched system of superficial lateral roots. The climbing part of the stem in immature plants is divided in a perennial, lignified region, and an annual dying one characteristic to semi-lignified plants. The climbing part of the stem in *P. natalensis* grows in length, with its perennial part increasing over time and, its annual part is formed only in the wet period. There is a slight increase in the diameter of the main root and the climbing part of the stem, as compared to juvenile plants. In representatives of *A. obesum,* due to the development of semisucculent climbing part of the stem, the determination zone between it and the more thickened BPS is less clear (Aviekin & Gaidarzhy 2017). A significant initial thickening of BPS can be further observed in immature rep-

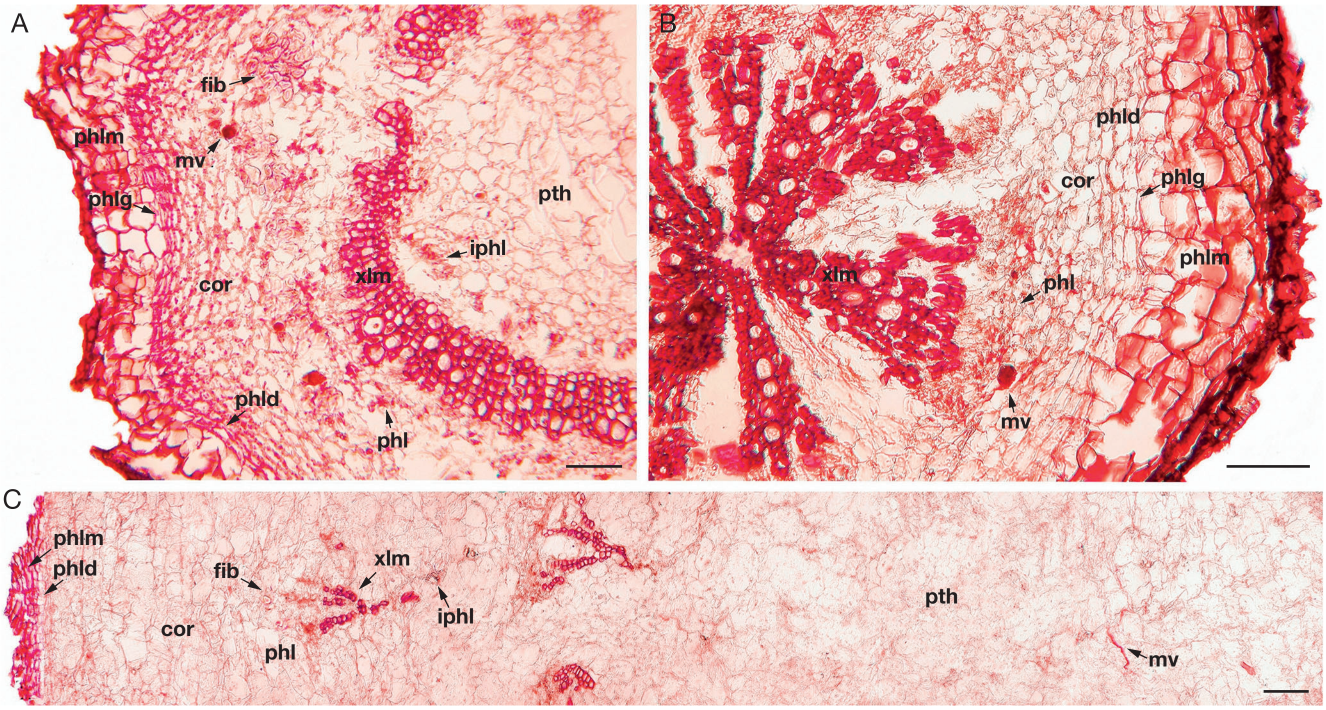

Fig. 6. — Anatomical structure of immature plants (1.5 year) of *Petopentia natalensis* (Schltr.) Bullock: **A**, apical part of stem; **B**, main root; **C**, basal part of stem. Abbreviations: **phlm**, phellem; **phld**, phelloderm; **fib**, sclerenchyma of phloem; **cor**, cortical parenchyma; **phl**, phloem; **xlm**, xylem; **pth**, pith; **iphl**, internal phloem; **mv**, milk vessels. Scale bars: A, B, 100 µm; C, 300 µm.

resentatives of *P. natalensis*, which becomes pear-shaped and is clearly demarcated as compared to other parts of the plants. Therefore, the BPS in immature plants of *P. natalensis* is formed exclusively from the expanded hypocotyl. Individual vascular-fibrous bundles in the BPS are tucked into the thicked pith, which is likely to supply water and nutrients to most deeper tissues. On the other hand, S. Carlquist (2018) noted that, in order to improve the water storage, succulents tend to show radially wider bands of axial parenchyma with thin walls, while the ray tissue amount is much greater than in the non-succulent species. The anatomical structure of BPS found in *P. natalensis* (Fig. 7B) clearly differs from that described in immature *A. obesum* individuals: in them, due to the active work of an interfascicular cambium, complete rings of conductive elements with well-developed xylem are formed (Fig. 7A).

In *P. natalensis* the secondary root structure is mainly distinguished by a highly lignified xylem, shaped as a polyarchic star at the tips of which the conducting elements of the phloem are located. However, in the main root of *A. obesum* immature plants, the situation is somewhat different, since the cambial meristem produces an abundant axial parenchyma, resulting in a thick radish main root (Aviekin & Gaidarzhy 2017). The extensive axial parenchyma distinctive of lianas is viewed as a pre-adaptation to water storage that facilitates succulence acquisition and thus shifts to arid climates (Hearn *et al.* 2018).

The comparison of the developments of *P. natalensis* and *A. obesum* illustrates two different developmental processes leading to succulence (Table 4).

CONCLUSION

The seeds of the endemic caudiciform plant of South Africa *Petopentia natalensis*, as well as the mesophytic representatives of the Apocynaceae family are characterized by a significant endosperm layer and a similar embryo structure. Formation of the expanded basal part of stem in *P. natalensis* begins in the juvenile period, unlike in *Adenium obesum* (Apocynaceae). The caudiciform part originated entirely from the hypocotyl part of the seedling, whereas in *A. obesum* mainly from the hypocotyl and root and to a lesser extent from the epicotyl. Seedlings have a similar bundle type of conductive tissues, but their subsequent development follows separate ways: bundle type of the conducting system in immature *P. natalensis* plants and non-bundle type in *A. obesum*.

Two different development strategies are used by these two species, therefore the issue of caudiciform formation requires further study on plants from other families to establish a clearer understanding.

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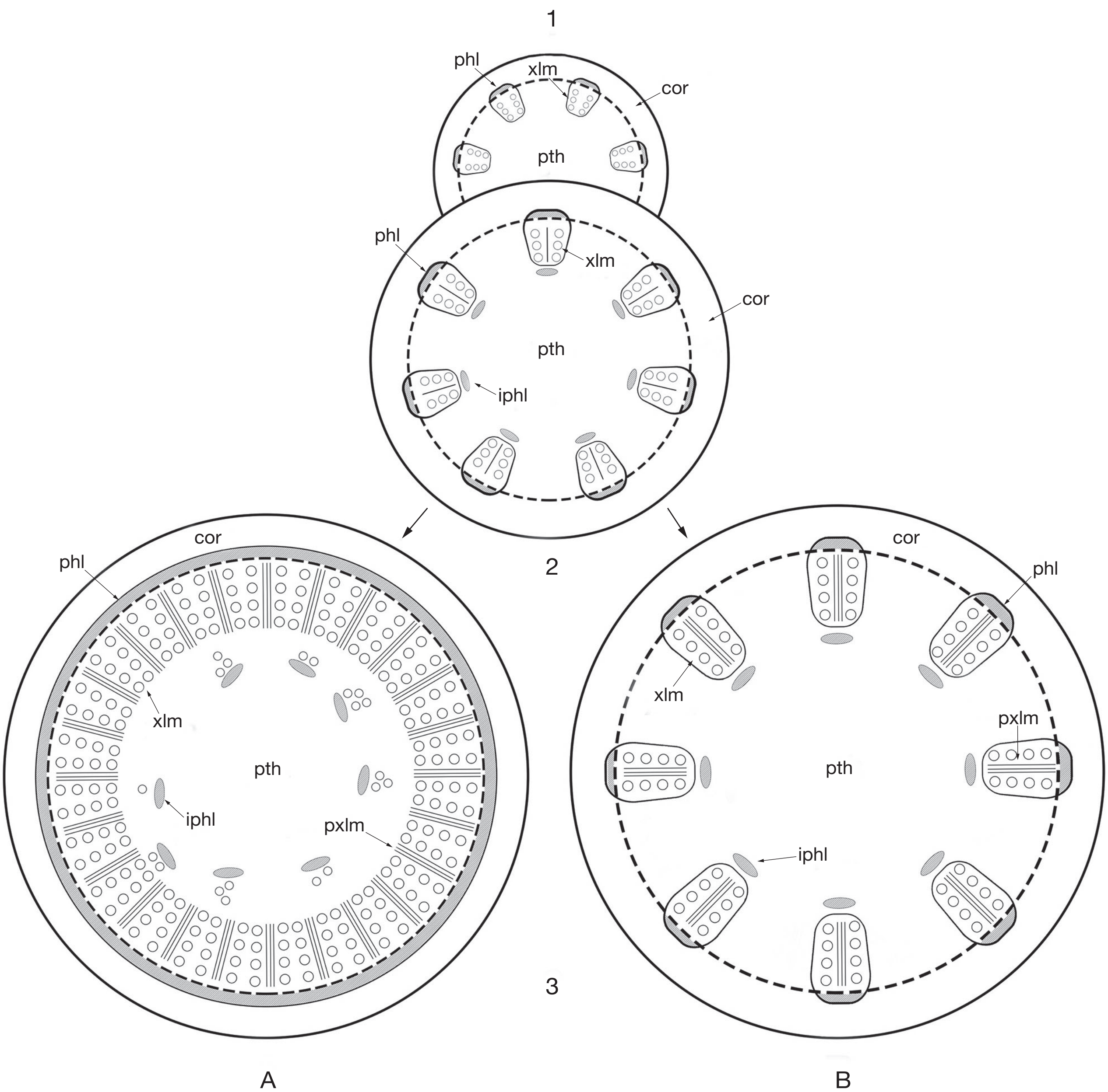

Fig. 7. — Development of conducting system at different ontogenetical stages (basal part of stem): **A**, *Adenium obesum* (Forssk.) Roem. & Schult.; **B**, *Petopentia natalensis* (Schltr.) Bullock; **1**, seedling; **2**, juvenile plant; **3**, immature plants. Abbreviations: **cor**, cortical parenchyma; **phl**, phloem; **xlm**, xylem; **pth**, pith; **iphl**, internal phloem; **pxlm**, xylem parenchyma.

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