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*Adansonia is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish: Geodiversitas, Zoosystema, Anthropozoologica, European Journal of Taxonomy, Naturae, Cryptogamie* sous-sections *Algologie, Bryologie, Mycologie, Comptes Rendus Palevol*

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Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40  
diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

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ISSN (imprimé / *print*): 1280-8571/ ISSN (électronique / *electronic*): 1639-4798

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Submitted on 3 October 2020 | accepted on 14 March 2021 | published on 19 October 2021

Tantawy M. E., Husein M. I., Mourad M. M. & Abdel-Hameed U. K. 2021. — Comparative floral anatomy of some species of Brassicaceae and its taxonomic significance. *Adansonia*, sér. 3, 43 (20): 223-234. <https://doi.org/10.5252/adansonia2021v43a20>. <http://adansonia.com/43/20>

## ABSTRACT

The diversity of the floral characters in 25 species of Brassicaceae representing seven tribes was studied through tracing their floral organs vascularization. The aim of the present study is to explore the contribution of the micro-floral characters in understanding the relationships among the studied species of Brassicaceae as well as the evolutionary trends in calyx, corolla, androecium and gynoecium. It was concluded that the vascularization of sepals, petals, stamens, nectaries and carpels was considered diagnostic and reliable characters at the specific level. The reduction and presence of vascular complexes was found to be at the top of the floral evolutionary trends. The micro-floral data were discussed in the view of dicta of evolution which facilitate the construction of proposed schematic presentation showing the line of advancement within each tribe. The line of advancement in tribe Brassicaceae (representing 14 studied species) is from the primitive *Raphanus sativus* L. to the advanced *Eruca sativa* Mill. To rule the line of evolution within other tribes, the number of studied taxa should be increased.

## RÉSUMÉ

*Anatomie florale comparée de quelques espèces de Brassicaceae et sa signification taxonomique.*

La diversité des caractères floraux de 25 espèces de Brassicaceae Burnett, représentant sept tribus, a été analysée à travers leur vascularisation florale. Cette étude visait à déterminer l'apport de la micromorphologie florale à la compréhension des relations interspécifiques, ainsi qu'à définir les tendances évolutives dans les différents verticilles. Il en ressort que la vascularisation tant des sépales, que des pétales, étamines, nectaires et carpelles peut fournir des caractères diagnostiques et fiables au niveau spécifique. L'évolution de la fleur est dominée par la réduction des structures et la formation corrélative de complexes vasculaires irriguant différents organes. Les résultats sont replacés dans un cadre évolutif schématisé, esquissant une ligne de progression pour chaque tribu, celle des Brassicaceae (14 espèces étudiées) pouvant être précisément tracée depuis *Raphanus raphanistrum* L. (état primitif) jusqu'à *Eruca sativa* Mill. (état avancé). Pour les autres tribus, un échantillonnage plus large de taxons apparaît indispensable.

**KEY WORDS**  
Cruciferae,  
Rhoedales,  
floral morphology,  
bicarpellary,  
tetracarpellary ovary,  
dicta of evolution,  
vascularization.

**MOTS CLÉS**  
Cruciferae,  
Rhoedales,  
morphologie florale,  
bicarpellaire,  
ovaire bicarpellé  
tétracarpellé,  
règles d'évolution,  
vascularisation.

TABLE 1. — The studied species of Brassicaceae and their localities. Localities: **A**, Ageba beach, Mersa Matruh, Egypt; **B**, Al-Bossaili region, Alexandria, Egypt; **C**, Alexandria-Mersa Matruh road, Egypt; **D**, around water irrigation canal, Kafr El-Sheikh, Egypt; **E**, Botanical Garden, Faculty of Science, Ain Shams University, Abbassia, Cairo, Egypt; **F**, Burg El-Arab and Mariut Regions, Alexandria, Egypt; **G**, Cairo-Suez road, Egypt; **H**, Damanhour agricultural road, around water irrigation canal, Egypt; **I**, Rashid district, Egypt; **J**, Seashore at Mersa Matruh, Egypt; **K**, Wadi El-Arbaeen, Saint Katherine, Egypt.

| No. | Species   | Localities     |
|-----|---|----------------|
| 1   | <i>Brassica nigra</i> (L.) K.Koch                     | F (Wild)       |
| 2   | <i>B. oleracea</i> L.                                 | D (Wild)       |
| 3   | <i>B. rapa</i> L.                                     | D (Wild)       |
| 4   | <i>B. tournefortii</i> Gouan                          | B (Wild)       |
| 5   | <i>Cakile maritima</i> Scop.                          | H (Wild)       |
| 6   | <i>Capsella bursa-pastoris</i> (L.) Medik.            | D (Wild)       |
| 7   | <i>Coronopus didymus</i> (L.) Sm.                     | D (Wild)       |
| 8   | <i>Didesmus bipinnatus</i> (Desf.) DC.                | I (Wild)       |
| 9   | <i>Diploaxis acris</i> (Forssk.) Boiss.               | E (Cultivated) |
| 10  | <i>D. harra</i> (Forssk.) Boiss.                      | C (Wild)       |
| 11  | <i>Eruca sativa</i> Mill.                             | F (Wild)       |
| 12  | <i>Erucaria crassifolia</i> (Forssk.) Delile          | H (Wild)       |
| 13  | <i>Farsetia aegyptia</i> Turra                        | K (Wild)       |
| 14  | <i>Lepidium sativum</i> L.                            | F (Wild)       |
| 15  | <i>Lobularia libyca</i> (Viv.) Webb & Berthel. Meisn. | B (Wild)       |
| 16  | <i>Matthiola incana</i> (L.) R.Br.                    | D (Wild)       |
| 17  | <i>M. livida</i> (Deille) DC.                         | F (Wild)       |
| 18  | <i>Matthiola longipetala</i> (Vent.)DC.               | E (Cultivated) |
| 19  | <i>Raphanus raphanistrum</i> L.                       | A (Wild)       |
| 20  | <i>R. sativus</i> L.                                  | D (Wild)       |
| 21  | <i>Rorippa islandica</i> (Oeder) Borbás               | G (Wild)       |
| 22  | <i>Schowwia thebaica</i> Webb                         | J (Wild)       |
| 23  | <i>Sisymbrium irio</i> L.                             | B (Wild)       |
| 24  | <i>S. orientale</i> L.                                | F (Wild)       |
| 25  | <i>Zilla spinosa</i> (L.) Prantl                      | F (Wild)       |

## INTRODUCTION

The floral vasculature has been accepted as a crucial method for studying the flower (Van Tieghem 1871). Subsequent workers raised more interest in that field of study and included it into an applicative form (Henslow 1891; Puri 1961; Tantawy *et al.* 2005; Mourad *et al.* 2015; Karakish *et al.* 2016) who shed light on the bases of floral micro-morphology as well as its importance in the elucidation of the floral macro-morphology, because sometimes the vestigial organs may be represented by their bundles, when any external trace of these organs has vanished, so the floral vasculature analysis can reveal the steps of evolution rather than the floral macro-morphology (Puri 1961).

Subramanyam & Narayana (1971) refined the point of view and stated that “simplicity represents reduced complexity”. In angiosperms as a whole, reduction is represented by such structures as a solitary stamen, the basal ovule, and the solitary microspores although these characters may be included within compound flowers. But the primitiveness or advancement of a simple structure can be clarified by the examination of the presence of vestigial vascular supplies. On the other hand, it is difficult to assume whether simplicity is a result of reduction and loss or fusion. External and even internal evidence of the fusion may be absent. The ontogeny, furthermore,

may be of no help because the fusion might have become fixed in phylogeny.

Full comprehension of evolutionary patterns and processes within Brassicaceae were not accomplished until the elapsed few years. Franzke *et al.* (2011) examined new outcomes from diverse botanical disciplines to synthesize an integrated view on the evolutionary history of the mustard family. For a conceivable perception of the evolutionary trends, the attention towards the study of character states should be followed (Stace 1980).

The carpel number of the gynoecium of Brassicaceae was a controversy subject long ago (Puri 1941). The tetracarpellary theory assumed that; the gynoecium is composed of four carpels; two sterile (valve) and two fertile carpels (solid), and the septum is true carpellary tissue, formed by the inward extension and subsequent fusion of the two fertile carpels. this theory was suggested by Eames & Wilson (1928), Dickson (1935), Merxmüller & Leins (1967). The bicarpellary theory assumed that; the gynoecium is composed of two carpels only, this theory was submitted by Arber (1931), Spratt (1932), Eggers (1935) and Zohary (1948). The bicarpellary theory was accepted by most botanists in spite of certain obvious difficulties in explaining the nature of the septum (Arber 1931; Spratt 1932).

The present study aimed to explore the contribution of micro-floral characters in understanding the relationships between the studied species and taxonomic trends among their tribes of Brassicaceae from evolutionary point of view according to Bessey’s dicta of evolution (Bessey 1915).

## MATERIAL AND METHODS

### SAMPLING

Flower buds of 25 species belonging to seven tribes were collected (according to Al-Shehbaz’s system of classification, 2012). The collected species and their localities are indicated in Table 1. The wild species were identified by the aid of Tackholm (1974) and Boulos (2005) while the horticultural species by Bailey & Bailey (1976) .

### FLORAL MICROMORPHOLOGICAL INVESTIGATION

The mature floral buds of the studied species were fixed in Formalin-Acetic acid-Alcohol solution (FAA), embedded in paraffin wax, then serially sectioned from pedicel upward at 10-15 µm according to Johansen (1940). The sections were double stained using safranin (2% in 50% ethanol) and light green (1% in absolute ethanol). Serial cross-sections from pedicel upwards in the mature flower bud of each species were drawn; drawings were made at bench level by the aid of “KEN-A-vision Microprojector” model X<sup>-</sup> 1000. The character states and evolutionary grades versus studied species data matrix was built in Table 2 based on Bessey (1915). A schematic placement for the species under investigation showing their evolutionary trends depending on the sum of the evolutionary grades was presented in Figure 3.

TABLE 2. — The Microfloral Characters and the Sum of the Evolutionary Points of the Studied Species of Brassicaceae.

| No.                            | Character                       | States   | 1  | 2  | 3  | 4  | 5 | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 |
|--------------------------------|---------------------------------|--|----|----|----|----|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1                              | Receptacle                      | Cont. (0), Diss. (1)   | 0  | 0  | 0  | 0  | 1 | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1  | 0  |
| 2                              | Ramification of sepal median    | Two only (0)<br>None of four (1)   | 0  | 0  | 0  | 0  | 0 | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  |
| 3                              | Sepal median nectarial complex  | Absent (0), Two (1),<br>Four (2)   | 1  | 2  | 2  | 1  | 1 | 0  | 0  | 1  | 1  | 0  | 1  | 1  | 1  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 2  | 1  | 2  | 2  | 1  |
| 4                              | Sepal marginal vascular sources | P.Sm.C only (0),<br>P.Sm.C and stele (1),<br>absent (2)  | 0  | 0  | 0  | 0  | 0 | 0  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 5                              | Petal complex                   | 1- or 2-organs (0), more<br>than 2 organs (1)  | 1  | 1  | 1  | 1  | 1 | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 1  | 1  | 1  | 1  | 1  |
| 6                              | Number of stamens               | Six (0), Two (1)   | 0  | 0  | 0  | 0  | 0 | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 7                              | Outer staminal bundles          | Solitary (0)<br>In complex (1)   | 1  | 0  | 0  | 1  | 0 | 0  | 0  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 0  |
| 8                              | Septum fusion                   | Fused (0), Partially<br>fused (1), Open (2)  | 0  | 1  | 2  | 2  | 0 | 1  | 2  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 2  | 0  | 1  | 1  | 1  | 0  | 0  |
| 9                              | Septum bundles                  | Present (0)<br>Absent (1)  | 0  | 1  | 0  | 1  | 0 | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 1  | 1  | 1  | 1  | 0  | 0  | 1  | 1  | 1  | 0  | 0  |
| 10                             | Lateral carpellary bundle       | Central stele (0), Dc.B.<br>(1)  | 0  | 1  | 0  | 0  | 0 | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  |
| 11                             | Ovules arrangement              | Parallel (0),<br>Alternating (1)   | 1  | 1  | 1  | 1  | 1 | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 1  |
| 12                             | Number of ovules                | Many (0), Two (1)  | 0  | 0  | 0  | 0  | 0 | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  |
| 13                             | Nectary type                    | Annular (0), 8-type (1)<br>4-type (2), 2-type (3)  | 2  | 2  | 2  | 2  | 2 | 2  | 2  | 2  | 2  | 2  | 2  | 2  | 3  | 2  | 1  | 3  | 3  | 3  | 2  | 2  | 0  | 2  | 0  | 0  | 2  |
| 14                             | Nectaries                       | All vascularized (0)<br>Some vascularized (1)  | 0  | 0  | 0  | 0  | 0 | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 0  |
| 15                             | Nectary vasculature sources     | One source (0),<br>two sources (1),<br>four sources (2),<br>six sources (3),<br>eight sources (4),<br>nine sources (5) | 4  | 4  | 4  | 4  | 3 | 2  | 2  | 3  | 4  | 2  | 5  | 3  | 2  | 2  | 2  | 1  | 1  | 1  | 3  | 0  | 4  | 4  | 4  | 4  | 3  |
| Sum of the evolutionary grades |                                 |  | 10 | 13 | 12 | 13 | 9 | 11 | 14 | 11 | 12 | 7  | 15 | 10 | 11 | 12 | 9  | 7  | 7  | 7  | 12 | 5  | 12 | 12 | 11 | 9  | 8  |

## ABBREVIATIONS

The abbreviations used for the floral vascularization are:

|             |   |
|-------------|---|
| Dc. B.      | dorsal carpellary bundle;               |
| Lc. B.      | lateral carpellary bundle;              |
| N.B.        | nectarial bundle;                       |
| N.T.        | nectarial tissue;                       |
| Ov.         | ovule;                                  |
| P.B.        | petal bundle;                           |
| P.S.Ma.C.   | petal sepal marginal complex;           |
| P.S.Ma.N.C. | petal sepal marginal nectarial complex; |
| S.M.B.      | sepal median bundle;                    |
| S.M.N.C.    | sepal median nectarial complex;         |
| S.Ma.B.     | sepal marginal bundle;                  |
| Spt.        | septum;                                 |
| Spt.B.      | septal bundle;                          |
| St.B.       | staminal bundle;                        |
| St.N.C.     | staminal nectarial complex;             |
| St.T.       | staminal trace;                         |
| Stg.        | stigma;                                 |
| Vc.B.       | ventral carpellary bundle.              |

## RESULTS

The behaviors of the organs vasculature in the studied taxa were represented in selected five species to illustrate the specific micro-floral characters and summarized in (Table 2); and (Figs 1-5), we observed the following vascular supply conditions:

## THE PEDICEL CONDITIONS

1) Continuous siphonosteles as in *Brassica nigra*, this behavior was observed in *B. oleracea*, *B. rapa*, *B. tournefortii*, *Matthiola incana*, *M. livida*, *M. longipetala*, *Schouwia thebaica* and *Zilla spinosa* (Fig. 1A); or 2) dissected siphonosteles as in *Raphanus sativus*, this behavior was observed in the remaining 16 studied species (Fig. 2A).

*The calyx conditions*

1) Two sepal median bundles emerge directly from central stele and two from sepal-median-nectarial complexes in 13 studied species (Fig. 1B-F); 2) Four sepal median bundles arise directly from the central stele as distinct sepal median traces, cut, migrate then enter the sepal tissue as one sepal median bundle. The sepal median bundles remain unramified in antero-posterior sepals and ramified within the two laterals in *Lobularia libyca*, *Raphanus raphanistrum* and *R. sativus* (Fig. 2B-F); 3) Four sepal median bundles from the central stele to four sepals without ramification throughout in *Capsella bursa-pastoris*, *Coronopus didymus*, *Diploaxis harra*, *Lepidium sativum* (Fig. 3B-D); or 4) Four sepal median bundles arise from sepal-median-nectarial complexes, cut and migrate through the receptacular tissue then enter as one sepal median bundle each (*Brassica oleracea*, *B. rapa*, *Rorippa islandica*, *Sisymbrium irio* and *S. orientale*) and the remaining of complexes represent vascular supply of nectaries (Fig. 4B-F).

### The corolla conditions

1) From petal-sepal marginal-nectarial complexes in 19 studied species (Fig. 1D-F); 2) From petal-sepal marginal complexes in *Farsetia aegyptia*, *Matthiola incana*, *M. livida*, *M. longipetala* and *Raphanus sativus* (Fig. 2C-E); or 3) Four petal vascular bundles protrude from petal-nectarial complexes in *Coronopus didymus* (Fig. 3C-E).

### The androecium conditions

All taxa have six stamens except *Coronopus didymus* and *Lepidium sativum* having two stamens only: 1) Six staminal bundles to six fertile stamens, the two outer stamens receive the vascular supply from two staminal-nectarial complexes while the four inner receive directly from the central stele in *Brassica nigra*, *B. tournefortii*, *Diplotaxis acris*, *Eruca sativa*, *Farsetia aegyptia*, *Raphanus raphanistrum* and *Schouwia thebaica* (Fig. 1D-G); 2) Six staminal bundles to six fertile stamens (two outer and four inner) emerge directly from the central stele in 13 studied species (Fig. 2D-I); or 3) Two staminal vascular bundles to two fertile stamens emerge directly from the central stele in *Coronopus didymus* and *Lepidium sativum* (Fig. 3, C-G).

### The gynoecium conditions

The remaining central stele is mainly differentiated into: 1) Ten vascular masses; two dorsal carpellary bundles, two ventral carpellary masses, four lateral carpellary bundles and two septal bundles in 12 studied taxa (Fig. 1I-M); 2) Eight vascular masses; two dorsal carpellary bundles, two ventral carpellary masses, four lateral carpellary bundles in *Brassica tournefortii*, *Matthiola incana*, *M. livida*, *M. longifolia*, *Schouwia thebaica* and *Sisymbrium irio* (Fig. 5I-L); 3) Six vascular masses, two dorsal carpellary bundles, two ventral carpellary masses, two septal bundles in *Coronopus didymus* & *Lepidium sativum* (Fig. 3F-K); or 4) Four vascular masses, two dorsal carpellary bundles and two ventral carpellary masses in *Brassica oleracea*, *Capsella bursa-pastoris*, *Farsetia aegyptia*, *Lobularia libyca* and *Rorripa islandica* (Fig. 4H-N). In the latest two conditions the lateral bundles derived from dorsal carpellary bundles by splitting.

### The septal conditions

The false septum is vascularized by two septal bundles (14 species) or non-vascularized in the rest 11 studied species. Septum completely fused (nine studied species), partially fused (12 species) or open (*Brassica rapa*, *B. tournefortii*, *Coronopus didymus* and *Raphanus raphanistrum*).

## DISCUSSION

Most taxonomists probably agreed in believing that not all characters are of equal importance in determining the degree of phylogenetic advancement of a group. On the other hand, considerable disagreement might exist with respect to which characters are most important and which one of less importance. Reversibly the states of each character can be evaluated from the phylogenetic point of view and consequently placed

into its respective position in the evolutionary sequence to mimic primitive position, an intermediate or advanced level. Thus, for each single character, the weight of its states had been determined on bases of the evolutionary dicta arrived at by several phylogenetic systems (Bessey 1915; Thorne 1958; Hutchinson 1959 and Smith 1967).

### TRENDS IN PEDICEL

The continuous siphonostele was regarded the basic case (classical) for the dissected siphonostele (advanced) based on the classical concepts of Bessey (1915), Hutchinson (1959) and Smith (1967).

### TRENDS IN CALYX

The vascular supply of the sepal in the majority of the studied species was in three-traced pattern (classical pattern). Each sepal receives three bundles from one origin (dependent case) or from different sources (independent case). The latter case was considered an advanced over the former case due to increase of complexity. Similar cases of vascularization were recorded in a large number of families; Boraginaceae (Al-Nowaihi *et al.* 1987), Polygonaceae (Tantawy *et al.* 2005), Nitrariaceae (Hussein *et al.* 2009), Scrophulariaceae (Mourad *et al.* 2015) and Crassulaceae (Karakish *et al.* 2016). Since the three-trace type was almost the basic one in the angiosperm from which modification could occur (Puri 1961), the single median bundle of the sepal throughout was considered the climax which is in accordance with the concept of absence altogether (Stebbins 1974).

The attributes of sepal vascularization in the present study reflected some facts. The majority of the species under investigation had the conventional number of sepal vascularization (one sepal median and two lateral bundles; the latter are absent in only one species). Such type was considered as the typical aspect (Puri 1961; Tantawy *et al.* 2005 and Karakish *et al.* 2016).

The sepal vascular supply was independent (from different sources) in 24 species or dependent (from one source) only in *Coronopus didymus*. The independent origin was considered a grade of advancement over dependent origin due to increase of complexity. This is in accord with Tantawy *et al.* 2005, Mourad *et al.* 2015 and Karakish *et al.* 2016.

### TRENDS IN COROLLA

The petal in all the studied species had a single trace. Similar aspect of vascularization achieved previously in different angiospermic families (Saunders 1934; Dickson 1935; Tantawy *et al.* 2005; Mourad *et al.* 2015). The deriving of petal vascular supply from complexes with other whorl was considered step toward advancement (due to the principle of complexity).

### TRENDS IN ANDROECIUM

Stamen received a single bundle throughout in all the species under investigation, which was considered the classical pattern. The unsplitting staminal bundle into the filament was considered an advanced case over the splitting of staminal bundle into three as in members of Musaceae (Bessey 1915).

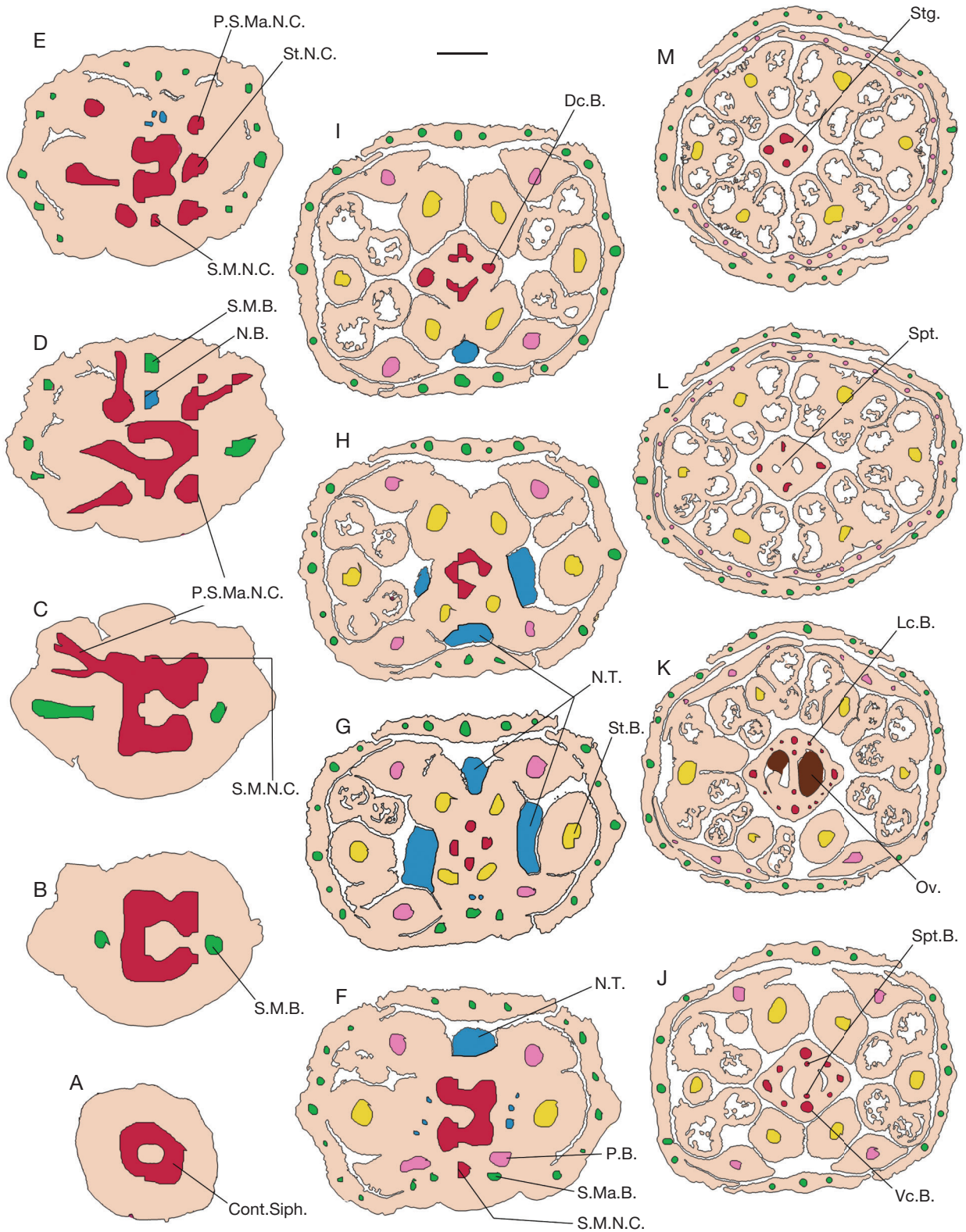


FIG. 1. — Serial cross sections from below upwards through a floral bud of *Brassica nigra* (L.) W.D.J.Koch showing: **A**, pedicel vasculature; continuous siphonostele; **B-F**, Calyx vasculature; two sepal median bundles emerge directly from central stele and two from sepal-median-nectarial complexes; **D-F**, corolla vasculature; from petal-sepal marginal-nectarial complexes; **D-G**, androecium vasculature; the two outer stamens receive the vascular supply from two staminal-nectarial complexes while the four inner receive directly from the central stele; **I-M**, gynoecium vasculature; ten vascular masses; two dorsal carpellary bundles, two ventral carpellary masses, four lateral carpellary bundles and two septal bundles. Scale bar: 200  $\mu$ m.

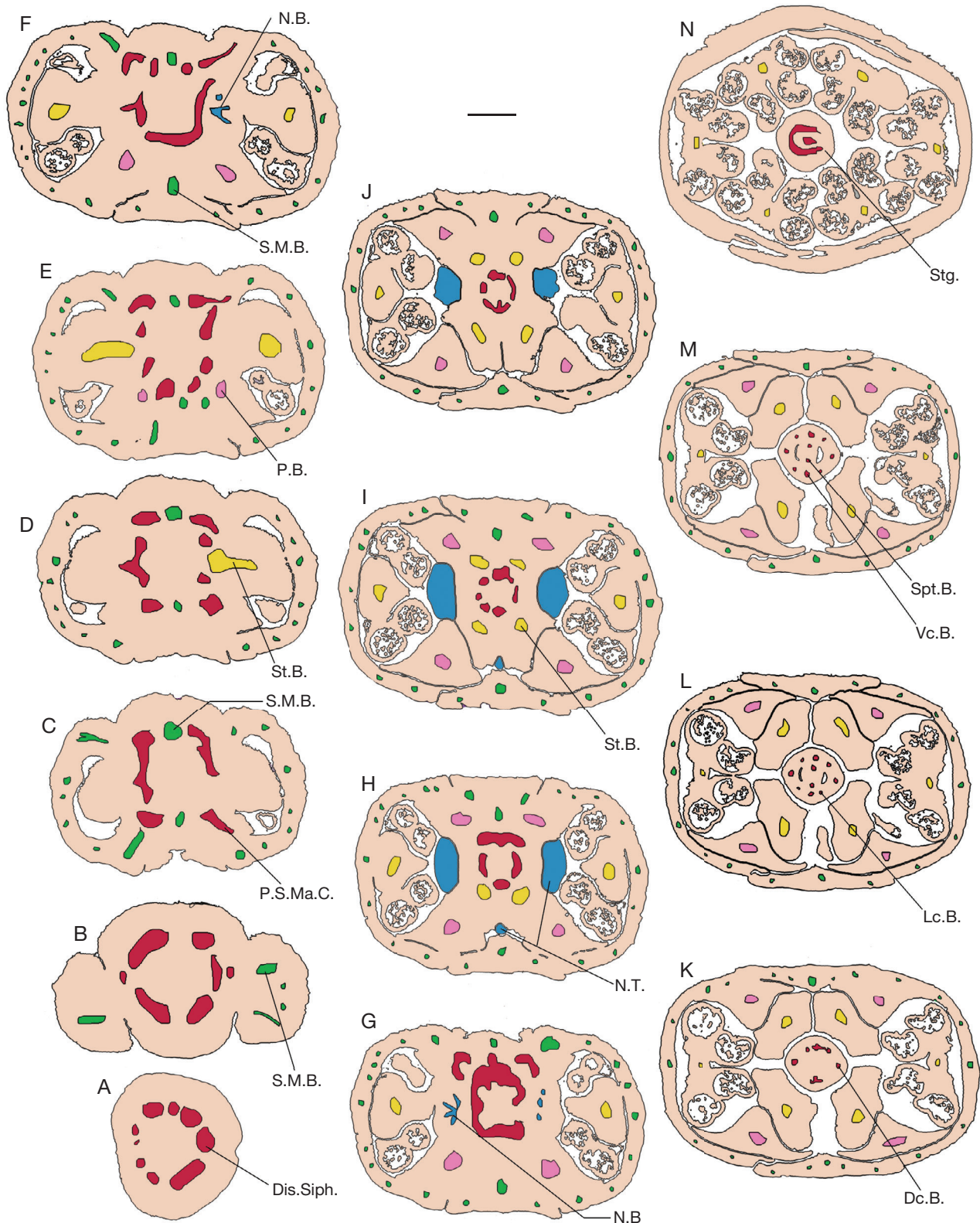


FIG. 2. — Serial cross sections from below upwards through a floral bud of *Raphanus sativus* L. showing: **A**, pedicel vasculature; dissected siphonostele; **B-F**, calyx vasculature; four sepal median bundles arise directly from the central stele as distinct sepal median traces, two antero-posterior ramified and two laterals unramified; **C-E**, corolla vasculature; from petal-sepal marginal complexes; **D-I**, androecium vasculature; six staminal bundles to six fertile stamens emerge directly from the central stele; **J-N**, gynoecium vasculature; ten vascular masses; two dorsal carpellary bundles, two ventral carpellary masses, four lateral carpellary bundles and two septal bundles. Scale bar: 500  $\mu$ m.



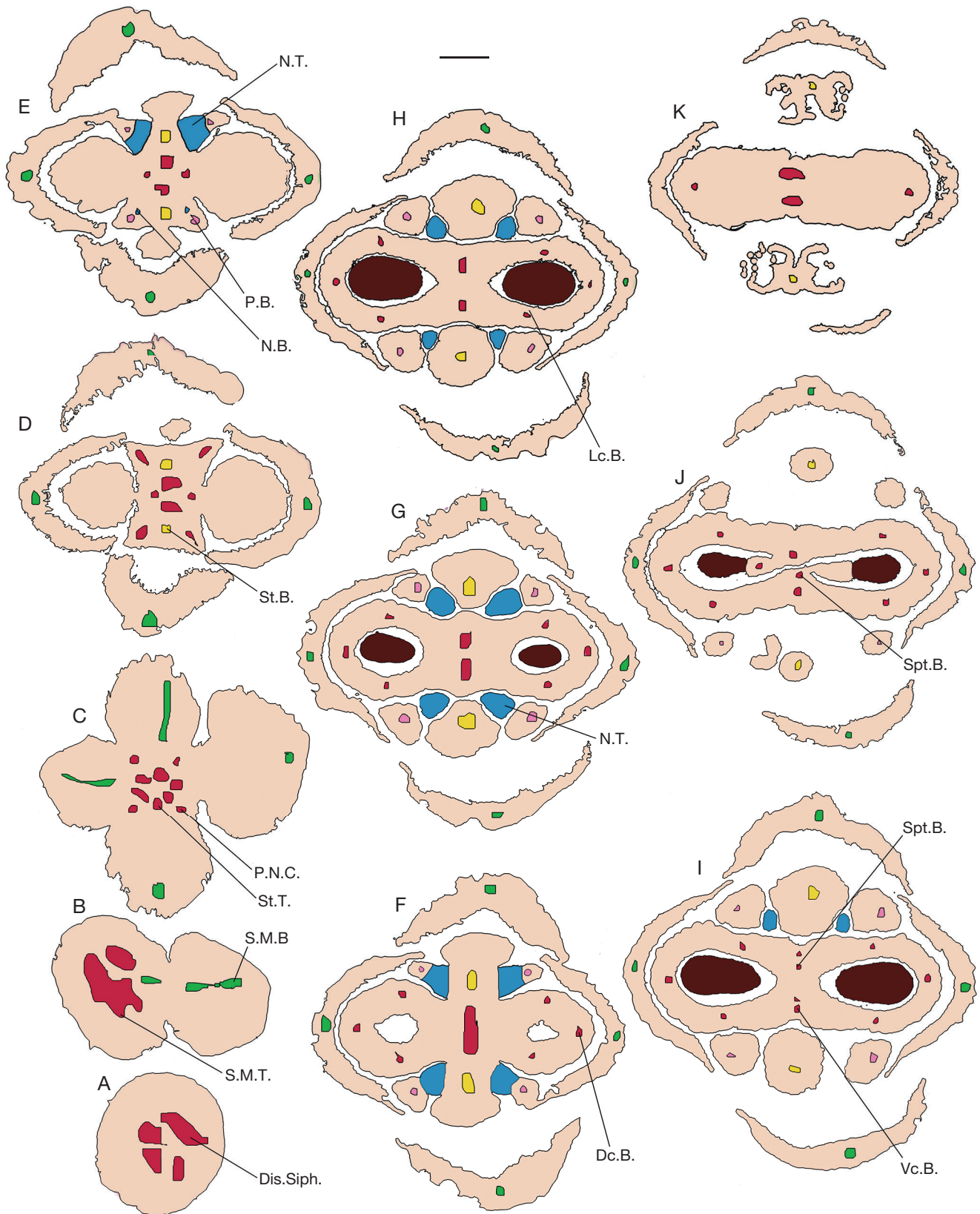


FIG. 3. — Serial cross sections from below upwards through a floral bud of *Coronopus didymus* (L.) Sm. showing: **A**, pedicel vasculature; dissected siphonostele; **B-D**, calyx vasculature; four sepal median bundles arise directly from the central stele as distinct sepal median traces without ramification; **C-E**, corolla vasculature; four petal vascular bundles protrude from petal-nectarial complexes; **C-G**, androecium vasculature; two staminal vascular bundles to two fertile stamens emerge directly from the central stele; **F-K**, gynoecium vasculature; six vascular masses, two dorsal carpillary bundles, two ventral carpillary masses, two septal bundles. Scale bar: 60  $\mu$ m.

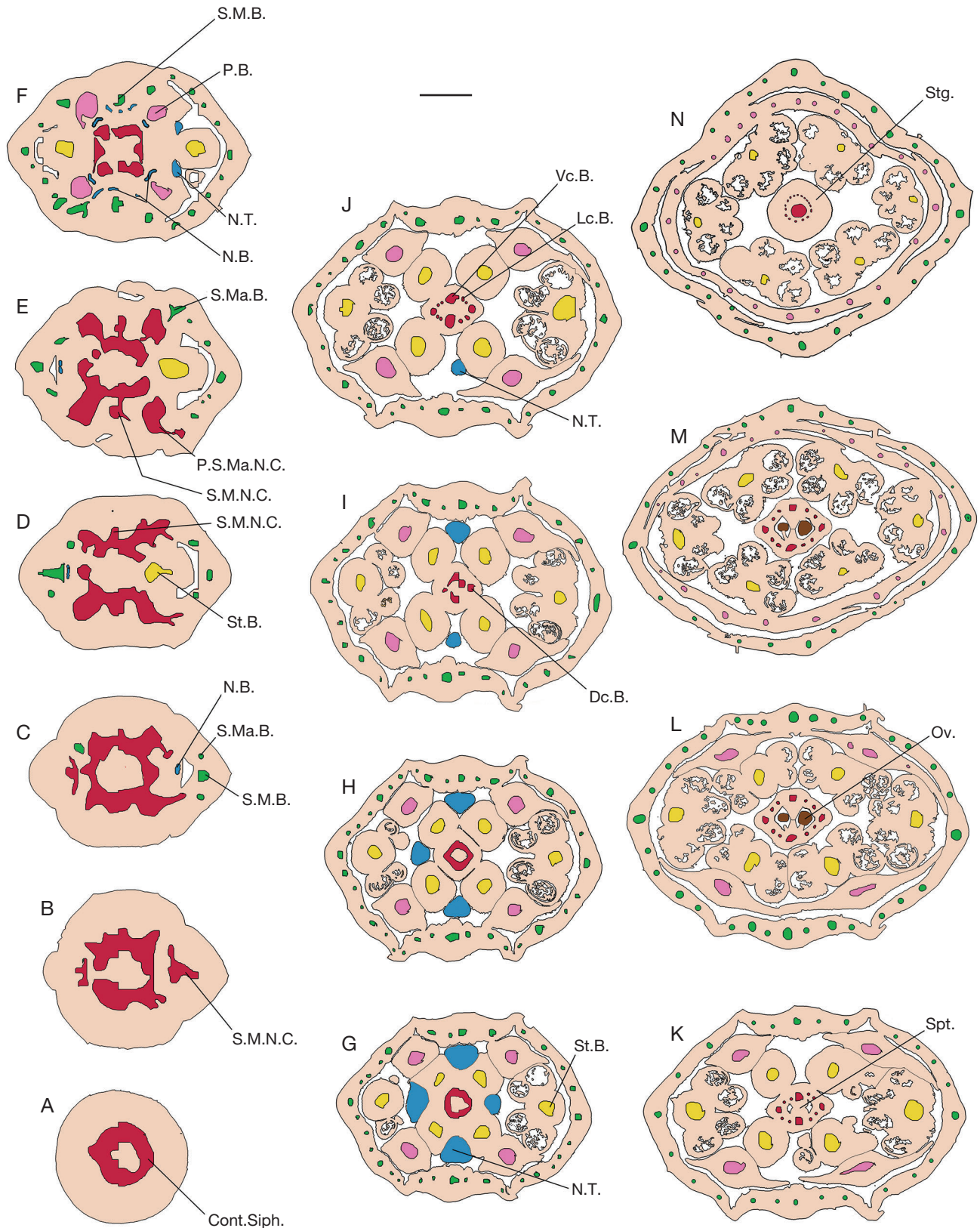


FIG. 4. — Serial cross sections from below upwards through a floral bud of *Brassica oleracea* L. showing: **A**, pedicel vasculature; continuous siphonostele; **B-F**, calyx vasculature; four sepal median bundles arise from sepal-median-nectarial complexes; **D-F**, corolla vasculature; from petal-sepal marginal-nectarial complexes; **D-G**, androecium vasculature; six staminal bundles to six fertile stamens emerge directly from the central stele; **H-N**, gynoecium vasculature; four vascular masses, two dorsal carpellary bundles and two ventral carpellary masses. Scale bar: 500  $\mu$ m.

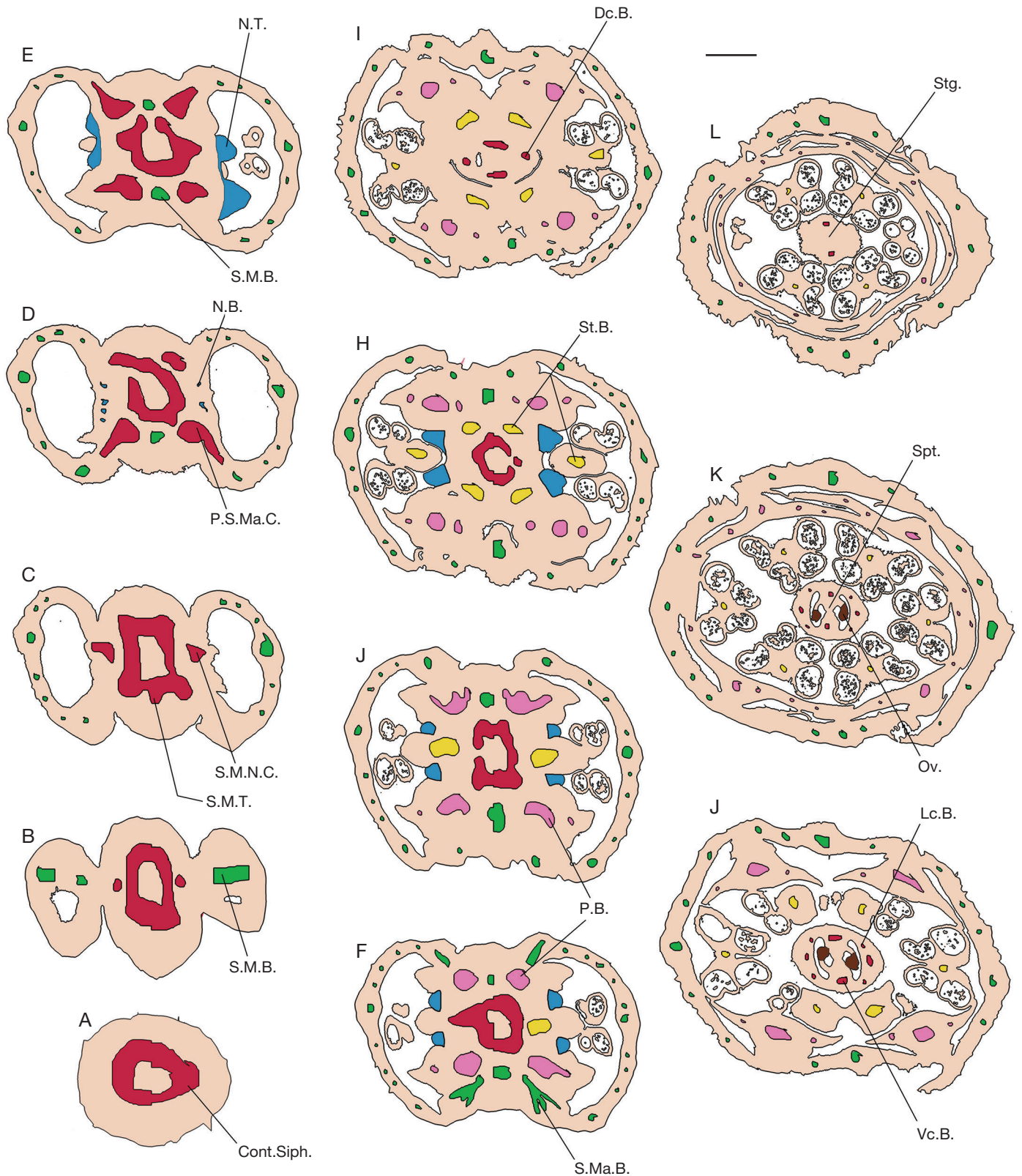


FIG. 5. — Serial cross sections from below upwards through a floral bud of *Matthiola incana* (L.) R.Br. showing: **A**, pedicel vasculature; continuous siphonostele; **B-F**, calyx vasculature; two sepal median bundles emerge directly from central stele and two from sepal-median-nectarial complexes; **D-G**, corolla vasculature; from petal-sepal marginal complexes; **D-H**, androecium vasculature; six staminal bundles to six fertile stamens emerge directly from the central stele; **I-L**, gynoecium vasculature, eight vascular masses; two dorsal carpellary bundles, two ventral carpellary masses, four lateral carpellary bundles. Scale bar: 500 µm.

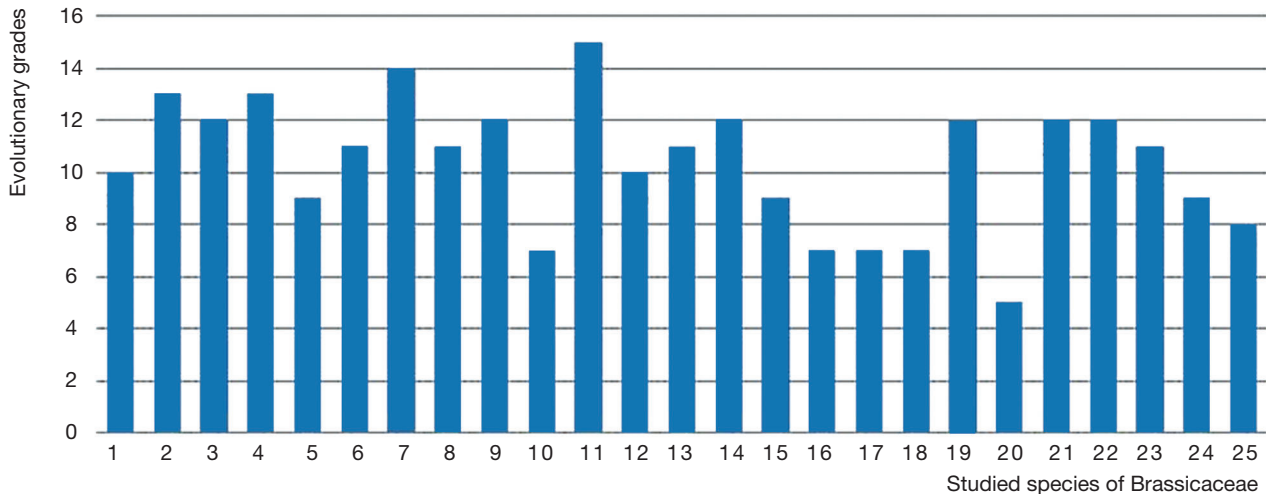


FIG. 6. — The evolutionary grades of the studied species of Brassicaceae.

In all the studied species, the ditheous anther condition was considered the primitive case in Brassicaceae (where the monotheous is an intermediate and staminode is the climax). As regards the number of stamens, number of vascular bundles and their origin, the studied species arranged in advanced pathway from, six fertile stamens with six bundles from one source (dependent) to six fertile stamens with six bundles from different sources (independent) to two fertile stamens with two bundles (the climax, whether dependent on independent). This is in accord with Stebbins (1974), Tantawy *et al.* (2005), Mourad *et al.* (2015) and Karakish *et al.* (2016).

According to Eames (1961), the evolutionary line is from full number of stamens to missing through suppression or abortion. So, the studied species with six stamens are on the bottom of the evolutionary ladder and those of two stamens are on the top. One more point might be added regarding to the floral symmetry; that the bilateral symmetry is an advance over radial symmetry. The phenomenon of abortion, suppression or missing altogether will lead to this advanced case (Stebbins 1974). Following this concept, the reduction of the staminal traces to two with the corresponding reduction in the morphological entities (two fertile stamens) as in *Coronopus didymus* and *Lepidium sativum* would be the climax. This is in accord with Tantawy *et al.* 2005 and Mourad *et al.* 2015.

#### TRENDS IN GYNOCIDIUM

The classical angiosperm carpel was supplied by three traces; one dorsal and two ventral carpellary bundles (Bessey 1915; Eames 1929; Fraser 1937; Eames & MacDaniels 1947; Puri 1961; Stebbins 1974). In the present study such three-veined condition was subjected by certain modification such as fusion of each pair of the four ventral carpellary bundles to form one ventral carpellary mass. The lateral and septal carpellary bundles might be present, emerged directly from the central stele or from dorsal carpellary bundles through splitting.

As regards the ventral supply, it could be stated that the separation of the two ventral bundles of each carpel (distinct

bundles) was the base while the fusion of the two carpellary ventral bundles (one from each carpel) was considered grade up. The data in the present study documented the second case and this is in accord with Bessey 1915, Stebbins 1974, Tantawy *et al.* 2005, Hussein *et al.* 2009 and Mourad *et al.* 2015.

It is necessary to say that the false septum is placental in nature developing from the ingrowth of the placenta, in contrast to the true septum that is carpellary in nature developing from the fusion of the carpellary wall (Hill & Lord 1989; Sessions & Zambryski 1995).

The data extracted from the number of carpels, vasculature pattern of gynoecium and septal vascular supply in the present study serve to bicarpellary theory in all studied species, where the cruciferous ovary receives two dorsal carpellary bundles and two ventral carpellary masses (each represents two fused ventral bundles for the adjacent carpels). This is in accord with Brückner (2000), who supported the bicarpellary theory.

From evolutionary point of view and in the view of Bessey's dicta of evolution, the line of advancement through the tribes can be summarized as follows:

#### Tribe Anastaticae

Due to the small number of species, authors unequivocally suggested that *Farsetia aegyptia* and *Lobularia libyca* occupied more or less an intermediate position in the direction of advancement, as they have a combination of advanced and primitive characters (Figs 6; 7).

#### Tribe Anchonieae

*Matthiola incana*, *M. livida* and *M. longipetala* exhibited number of primitive characters *viz.* continuous siphonostele, ramified sepal median bundles, sepal marginal bundles, dependent petal supply derived from one source (complex), six staminal bundles to six fertile stamens, outer staminal bundles from central stele, fused septum, lateral carpellary bundles derived from the central stele, many ovules and vascularized nectaries. This is in agreement with Al-Shehbaz (1989). For all the foregoing characters, tribe Anchonieae occupied a less advanced level (Figs 6; 7).

|       |                          |                       |   |                                |                          |                          |                        |
|-------|--------------------------|-----------------------|---|--------------------------------|--------------------------|--------------------------|------------------------|
| 15    |                          |                       | <i>Eruca sativa</i>   |                                |                          |                          |                        |
| 14    |                          |                       |   |                                |                          | <i>Coronopus didymus</i> |                        |
| 13    |                          |                       | <i>Brassica oleracea</i><br><i>B. tournefortii</i><br><i>B. rapa</i>                |                                |                          |                          |                        |
| 12    |                          |                       | <i>Diplotaxis acris</i><br><i>Raphanus raphanistrum</i><br><i>Schouwia thebaica</i> |                                | <i>Rorippa islandica</i> | <i>Lepidium sativum</i>  |                        |
| 11    | <i>Farsetia aegyptia</i> |                       | <i>Didesmus bipinnatus</i>  | <i>Capsella bursa-pastoris</i> |                          |                          | <i>Sisymbrium irio</i> |
| 10    |                          |                       | <i>B. nigra</i><br><i>Erucaria crassifolia</i>                                      |                                |                          |                          |                        |
| 9     | <i>Lobularia libyca</i>  |                       | <i>Cakile maritima</i>  |                                |                          |                          | <i>S. orientale</i>    |
| 8     |                          |                       | <i>Zilla spinosa</i>  |                                |                          |                          |                        |
| 7     |                          | <i>Matthiola spp.</i> | <i>D. harra</i>   |                                |                          |                          |                        |
| 6     |                          |                       |   |                                |                          |                          |                        |
| 5     |                          |                       | <i>Raphanus sativus</i>   |                                |                          |                          |                        |
| 4     |                          |                       |   |                                |                          |                          |                        |
| 3     |                          |                       |   |                                |                          |                          |                        |
| 2     |                          |                       |   |                                |                          |                          |                        |
| 1     |                          |                       |   |                                |                          |                          |                        |
| Tribe | Anastaticae              | Anthonieae            | Brassicaceae  | Camelinaeae                    | Cardamineae              | Lepidieae                | Sisymbrieae            |

Fig. 7. — Schematic placement showing the evolutionary trends of the studied species of Brassicaceae based on floral morphology (Al-Shehbaz 2012).

#### Tribe Brassiceae

The line of advancement was from *Raphanus sativus* (less advanced) to *Eruca sativa* (advanced) through the intermediate level (12 studied species). *Eruca sativa* exhibits number of advanced characters *viz.* dissected siphonostele, unsplitting sepal median bundles throughout, the petals vascular supply derived from complexes, the two outer staminal bundles arose from complex shared with nectaries and non-vascularized septum. The primitiveness of *Raphanus sativus* was owing to the sepal median bundles arose from the central stele with further ramification (dependent origin), dependent sepal marginal bundles, petal bundles come from complexes sharing with one organ, fused vascularized septum, the lateral carpellary bundles from the central stele, many ovules and vascularized nectaries (Figs 6; 7).

#### Tribe Camelinaeae

It could not be ruled because only *Capsella bursa-pastoris* was studied. It had a combination of primitive and advanced characters (Figs 6; 7).

#### Tribe Cardamineae

Due to the small number of species, authors unreliably suggested that *Rorippa islandica* had some of advanced characters *viz.* dissected siphonostele, unramified sepal median bundles emerged from complexes, the petal bundles shared in complexes with two organs, non-vascularized septum and the lateral carpellary bundles derived from the dorsal carpellary bundles (Figs 6; 7).

#### Tribe Lepidieae

Due to the small number of species, authors unreliably suggested that *Coronopus didymus* and *Lepidium sativum*, oc-

cupied an advanced level. *Coronopus didymus* showed a wide range of advanced characters *viz.* dissected siphonostele, sepal median bundles remain one throughout (uni-nerved), two fertile stamens, septum opened, the lateral carpellary bundles come from dorsal carpellary bundles and two alternating ovules (Figs 6; 7).

#### Tribe Sisymbrieae

Due to the small number of species, authors unreliably suggested that the evolutionary line could not be ruled easily because *Sisymbrium irio* and *S. orientale* occupied more or less an intermediate position because they had a combination of primitive and advanced characters (Figs 6; 7).

## CONCLUSION

The floral vascularization of sepals, petals, stamens, nectaries and carpels was considered as diagnostic and reliable characters at the specific level. The line of advancement in tribe Brassiceae was from the most primitive species: *Raphanus sativus* to the advanced one: *Eruca sativa*, to rule the line of evolution within other tribes of Brassicaceae, the number of studied taxa should be increased. The number of carpels, vasculature pattern of gynoecium and septal vascular supply in the present study supported the bicarpellary theory in Brassicaceae.

## Acknowledgements

The authors thank Thierry Deroin and an anonymous referee for their comments on a previous version of the manuscript.

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Submitted on 3 October 2020;  
accepted on 14 March 2021;  
published on 19 October 2021.