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Morphology and molecules support the new monotypic genus *Parainvolucrella* (Rubiaceae) from Asia

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Abstract
Parainvolucrella R.J. Wang, a new monotypic genus is segregated from *Hedyotis-Oldenlandia* complex based on the morphological and molecular evidences, along with the new combination of *P. scabra* (Wall. ex Kurz) M.D.Yuan & R.J.Wang. The new genus is phylogenetically sister to *Scleromitrion* and has ever been mistaken as a member of *Scleromitrion*, but its perennial woody herbaceous habit, terminal inflorescence, heterostylous flowers, indehiscent capsules, and microreticulate with smooth muri pollen surface ornamentation make it different from the latter. A key for all the genera of this complex in China is provided as well.

Keywords
new combination, palynology, *Parainvolucrella*, Rubiaceae, taxonomy

Introduction
As one of the largest species groups of the family Rubiaceae, *Hedyotis-Oldenlandia* complex contains hundreds of species distributed in the tropical and subtropical region worldwide. Due to the morphological intermediacy and homoplasy, systematic studies in herbaceous Rubiaceae is difficult to carry on (Gibbons 2020), the generic delimitation within this complex is complicated and controversial (Neupane et al. 2015) and historically disputed between the “lumpers” (Lamarck 1792; Fosberg and Sachet 1991; Dutta and Deb 2004; Chen and Taylor 2011) and the “splitters” (Bremekamp 1952; Terrell et al. 1986; Terrell and Robinson 2003). The commonly shared morphological characters, such as 4 petals and calyx lobes, 2-celled ovary with numerous ovules on an axile placentation and capsular fruits made the “lumpers” treat this complex as one genus *Hedyotis* in broad sense. On the other hand, the morphological differences in the habit, inflorescence position, homo- or heterostylous flowers, dehiscent or indehiscent capsules, as well as the shape and ornamentation of seeds and pollens provided the unquestionable evidence for “splitters” to separate this complex into several small genera. Recent phylogenetic analyses based on multiple nuclear and chloroplast DNA sequences revealed that this complex was polyphyletic and supported the subdivision of this complex into some small genera (Terrell and Wunderlin 2002; Terrell and Robinson 2007; Neupane et al. 2009; Guo et al. 2013; Wikström et al. 2013; Neupane et al. 2015; Gibbons 2020). Under this taxonomic treatment framework, the *Hedyotis* species in China will fall into the genera of *Debia*

Neupane & N.Wikstr., *Dimetia* (Wight & Arn.) Meisn., *Edrastima* Raf., *Hedyotis* L., *Involucrella* (Benth. & Hook.f.) Neupane & N.Wikstr., *Leptopetalum* Hook. & Arn., *Oldenlandia* L. and *Scleromitrion* (Wight & Arn.) Meisn. (Neupane et al. 2015; Wang 2018).

During our field investigation in Guangxi Zhuang Autonomous Region, we came across the species *Hedyotis scabra* Wall. ex Kurz in the bamboo forest nearby Nonggang National Nature Reserve. This plant is similar to *Involucrella coronaria* (Kurz) Neupane & N.Wikstr. because of its terminal inflorescence subtended by 4 bract-like leaves.

Neupane *et al*. (2015) made a nomenclature change to ascribe *Hedyotis scabra* to *Scleromitrion scabrum* (Wall. ex Hook.f.) Neupane & N.Wikström, but this taxonomic treatment was obviously improper because *Hedyotis scabra* was apparently not a member of the *Scleromitrion* clade, according to their ML phylogenetic tree. In addition, the basionym, *Hedyotis scabra* Wall. ex Hook. f. (1891), of this combination is a later homonym of *Hedyotis scabra* Wall. ex Kurz (1877) and should be illegitimate according to ICN.

Our further examination also revealed that the morphological characters of *Hedyotis scabra* are indeed incongruent with those of *Scleromitrion* in inflorescence position, flower distyly and the capsule dehiscence. Additional phylogenetic analysis based on the multiple DNA regions supported that this species represented a new genus and then described herein.

Materials and methods

Morphological characters of *Hedyotis scabra* were measured from the living materials and dried specimens. All the vouchers we collected were deposited at the herbarium of South China Botanical Garden, Chinese Academy of Sciences (IBSC). Pollens and seeds were observed using Scanning Electron Microscope (JSM-6360LV) under 15.00 kV accelerating voltage. Pollen terminology for description followed Hesse et al. (2009).

The methods of DNA extraction, PCR experiment methods followed Guo et al. (2011). Sequences of other taxa were downloaded from GenBank for molecular phylogenetic analysis (Table 1). GENEIOUS v11.0.3 (Kearse et al. 2012) was used for sequence alignment, MRMODELTEST 2.0 was applied for selecting the best model (GTR+G+I) on the basis of the AIC criterion (Nylander 2004). For Bayesian inference (BI) analyses, MRBAYES v3.2.7 (Ronquist et al. 2012) was chosen for phylogenetic simulation.

Results

Phylogenetic analysis

The phylogenetic analysis based on the nuclear ITS and four chloroplast DNA regions

(*pet*D, *rps*16, *trn*H-*psb*A and *trn*L-F) generated the almost similar tree to that of Neupane *et al*. (2015). It showed that all the samples of *Hedyotis scabra* cluster into an isolated clade which is sister to the *Scleromitrion* with robust support value (PP=1, Fig. 4). In addition, the *Involucrella* clade is a little phylogenetically far away from *Hedyotis scabra*, despite the morphological similarity between *I. coronaria* and *H. scabra* in having the terminal inflorescence subtended by 4 bract-like leaves.

Morphological comparison

The monomorphic and dimorphic of flowers, the shape, texture and dehiscent pattern of the capsule are of diagnostic significance in the different genera of *Hedyotis-Oldenlandia* complex (Dutta and Deb 2004). Our morphological observation lasting for several months found that the capsules of *Hedyotis scabra* are completely indehiscent, which was obscurely diagnosed by Hooker (1880) and wrongly described by Dutta and Deb (2004).

Comparing to the genus *Scleromitrion*, *Hedyotis scabra* has perennial woody herbaceous (vs. annual herbaceous in *Scleromitrion*) habit, terminal (vs. axillary or terminal and axillary in uppermost leaf axils in *Scleromitrion*) inflorescence, heterostylous (vs. homostylous in *Scleromitrion*) flowers, indehiscent (vs. loculicidally dehiscent in *Scleromitrion*) capsules.

Although *Involucrella* has dimorphic flowers and indehiscent or loculicidally dehiscent capsules, it still can be distinguished from *H. scabra* in erect or decumbent small herbaceous (vs. decumbent woody herbaceous) habit, ellipsoidal or oblate and no angles (vs. subglobose with 4 angles when young) capsules, ellipsoidal and 3–5 pitted (vs. trigonous with no pits on the surface) seeds.

The pollens of *Hedyotis scabra* are monads, isopolar, and spheroidal, with 3-colporate apertures, surface microreticulate, with smooth muri. The pollen size is 22.2 (20.9–23.7) × 20.2 (18.3–21.8) μm with P/E value 1.10 in short-styled flowers (Fig. 2A–C) and 20.2 (18.5–21.2) × 19.0 (16.6–20.6) μm with P/E value 1.06 in long-styled flowers (Fig. 2D–F). Comparing to *Scleromitrion*, the pollen ornamentation of *Hedyotis scabra* is microreticulate with smooth muri, however, it is rugulate with microechinate muri in *Scleromitrion*.

Taxonomic treatmens

Based on the much morphological and palynological differences between *Hedyotis scabra* and *Scleromitrion*, as well as the molecular evidence, a new genus is therefore proposed herein.

Parainvolucrella R.J. Wang, gen. nov. 拟合叶耳草属 (ni he ye er cao shu)

Parainvolucrella scabra (Wall. ex Kurz) M.D. Yuan & R.J. Wang, comb. nov., Figs 1–3.

Basionym: *Hedyotis scabra* Wall. ex Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 46(2): 133, 136 (1877). **Type**: MYANMAR**.** from Martaban down to Upper Tenasserim, *Wall. Cat. 880* (holotype: K [K000031881!]; isotypes: G [G00436284!; G00436285!]; K [K001110148!; K001110149!]).

Description. Perennial herbs or subshrubs, woody, branched, decumbent, to ca. 50 cm tall. Stems angular, scabrid. Leaves opposite, 2.0–7.0 × 1.0–3.0 cm, ovate to lanceolate, apex acute, base narrowly cuneate to cuneate; leaf deep green and scabrid adaxially, grayish green and more scabrid abaxially; midrib depressed adaxially and prominent abaxially, secondary veins 5–6 on each side, adaxially indistinct; petiole to 3 mm. Stipules ca. 3.0 × 2.0 mm, papery, triangular, margin pectinately glandular serrated, excurved, pubescent adaxially and glabrous abaxially. Inflorescence terminal, few flowered, capitate umbel, peduncles ca. 0.5 mm long, enclosed by usually 4 leaves, bracts lanceolate, 2–3 mm long, scabrid. Flowers heterostylous, pedicel to 0.8 mm. Hypanthium ca. 0.8 mm long, obconic, with 4 indistinct thickened angles; lobes 4, ca. 1.5 mm long, lanceolate, pubescent along the angles and lobes. Corolla white, tube 1.5–2.0 mm long, glabrous abaxially and tomentose adaxially at throat and the base of lobes; lobes 4, 2.3–2.8 × 0.7–0.8 mm, oblong. Stamens 4, anthers 0.6–0.7 mm long. Stigma bilobed, 0.5–0.6 mm long, papillate. Long-styled flowers: stamens included, filaments adnate to the base of corolla tube, filaments ca. 2 mm long; styles ca. 4.3 mm long, exserted, included part pubescent, stigma ellipsoid. Short-styled flower: stamens included; filaments adnate to the base of corolla tube, filaments ca. 5.6 mm long; styles ca. 2 mm long, exserted, pubescent, stigma clavate. Fruits capsular, 4-angled when young, ca. 2.1 × 2.3 mm, subglobose, with calyx lobes to 4.6 mm long, scabrid along the angles and calyx lobes, indehiscent. Seeds trigonous, 0.4–0.5 mm, numerous, black, with reticulate surface.

Phenology. Flowering from July to September; fruiting from October to December.

Etymology. The generic name "*Parainvolucrella*" refers to the terminal inflorescence subtended by 4 bract-like leaves, which is similar to that of *Involucrella coronaria*.

Distribution and habitat. Bangladesh, India, Myanmar, Thailand, and Vietnam (Fukuoka 1970, Dutta & Deb 2004), new record to China. Only one subpopulation including about 200 individuals was found in dense bamboo forest and at the edge of the forest nearby Guangxi Nonggang National Nature Reserve. The habitat there belongs to tropical monsoon climate, main associated species are *Dendrocalamus latiflorus* Munro (Poaceae) and *Centotheca lappacea* (L.) Desv. (Poaceae).

Additional specimens examined.
CHINA. **Guangxi Zhuang Autonomous Region:** Chongzuo City, Longzhou County, Zhubu Town, Nonggang Village, 1 Nov 1978, Nonggang Investigation Team 11263

(IBK!); same locality, 22 °29'16"N; 106 °56'13"E, elev. 287m, 29 Oct 2020, Ming-Deng Yuan & Yi-Da Xu YS398, YS399 (IBSC!); same locality, 22 °29'22"N; 106 °56'11"E, elev. 290m, 2 Feb 2021, Ming-Deng Yuan YS407 (IBSC!); Zhubu Town, Lenglei Village, 9 Oct 1979, Nonggang Investigation Team 20457 (GXMI!). THAILAND. **Kampeng:** Me Sawt, 25 Jun 1922, A.F.G. Kerr 6161 (SING!).

Notes. It was Kurz (1877), not Hooker (1880), who first legitimately published the name *Hedyotis scabra*. Therefore, the names of *Hedyotis scabra* Wall. ex Hook.f., *Oldenlandia scabra* (Wall.) Kuntze and *Scleromitrion scabrum* (Wall. ex Hook.f.) Neupane & N. Wikstr. are all illegitimate according to the articles 6.10 and 53.1 of ICN (Turland et al. 2018).

Key to the genera of *Hedyotis-Oldenlandia* complex in China

1 Perennial herbs, subshrubs or shrubs **2**
- Annual herbs **4**
2 Stipules basally connate, apex truncate, margin acicular spinous ..... ***Dimetia***
- Stipules triangular, ovate or obtrapezoid, margin sparsely glandular serrate or pectinate **3**
3 Capsules dehiscent diplophragmously (indehiscent in *Hedyotis baotingensis*, *H. cryptantha*, *H. paridifolia*, *H. prostrate* and *H. yazhouensis*) ..... ***Hedyotis***
- Capsules indehiscent ..... ***Parainvolucrella***
4 Inflorescences terminal or terminal and subapical axillary **5**
- Inflorescences axillary (terminal and subapical axillary in *Scleromitrion pinifolium* and *S. koanum*) **7**
5 Leaves clustered or 4-verticillate at uppermost ..... ***Debia***
- Leaves opposite at uppermost **6**
6 Corolla throat constricted; capsules 4-angled, winged ..... ***Leptopetalum***
- Corolla tubular or campanulate, throat not constricted; capsules ellipsoidal, subglobose or oblate ..... ***Involucrella***
7 Leaves ovate, elliptic to orbicular; capsules oblate, hairy ..... ***Edrastima***
- Leaves linear, linear-lanceolate to lanceolate; capsules ellipsoidal to subglobose, glabrous **8**
8 Stamens and stigma included in corolla tube ..... ***Oldenlandia***
- Stamens and stigma exserted from corolla tube ..... ***Scleromitrion***

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Table 1. Taxa, vouchers, localities, and GenBank accession numbers of ITS, *pet*D, *rps*16, *trn*H-*psb*A and *trn*L-F sequences for phylogenetic analysis.

Taxon	**Voucher (herbarium)**	**ITS**	***pet*D**	***rps*16**	***trn*H-*psb*A**	***trn*L-F**
Batopedina pulvinellata Robbr.	Zambia: Dessein et al. 264 (BR)	AM266989	EU557684	EU543021	/	EU543083
Debia ovatifolia (Cav.) Neupane & N. Wikstrom	China: Xing Guo et al. 20-1 (IBSC)	JF699940	JF700090	JX111309	JF699795	JX111382
Dimetia ampliflora (Hance) Neupane & N. Wikstrom	China: Ruijiang Wang et al. 1147 (IBSC)	JX111198	JX111086	JX111242	JX111161	JX111317
Dimetia auricularia (L.) R.J. Wang	China: Ruijiang Wang 1185 (IBSC)	JF699904	JF700053	JX111298	JF699765	JX111372
Dimetia capitellata (Wall. ex G. Don) Neupane & N. Wikstrom var. *capitellata*	China: Xiangxu Huang et al. GBOWS1278 (IBSC)	JX111201	JX111089	JX111250	JX111164	JX111327
Dimetia scandens (Roxb.) R.J. Wang	China: Ping Yang et al. 10 (IBSC)	JF699949	JF700099	/	JF699804	/
Edrastima trinervia (Retz.) Neupane & N. Wikstrom	Sri Lanka: F. Fagerlind 4338 (S)	HE657769	HE657652	HE649907	/	/
Hedyotis acutangula Champ. ex Benth.	China: Ruijiang Wang HA-02 (IBSC)	JX111197	JX111085	JX111241	JX111160	JX111316
Hedyotis cantoniensis F.C. How ex W.C. Ko	China: Ruijiang Wang et al. 1250 (IBSC)	JF976484	JF700061	JX111247	JF699773	JX111322
Hedyotis caudatifolia Merr. & F.P. Metcalf	China: Ruijiang Wang et al. 1269 (IBSC)	JF699916	JF700065	JX111256	JF699777	JX111329
Hedyotis effusa Hance	China: Ruijiang Wang et al. 1268_1 (IBSC)	JF699933	JF700083	JX111262	JF699790	JX111335
Hedyotis hainanensis (Chun) W.C. Ko	China: Guobing Jiang & Xinxin					

	Zhou 1121 (IBSC)					
Hedyotis ovata Thunb. ex Maxim.	China: Dan Liang et al. 1508 (IBSC)					
Hedyotis shenzhenensis T. Chen	China: Ruijiang Wang et al. 1262-1 (IBSC)	JF976502	JF700101	JX111276	JF699805	JX111350
Hedyotis uncinella Hook. & Arn.	China: Ruijiang Wang 1217 (IBSC)	JF699963	JF700113	JX111282	JF699814	JX111356
Involucrella chereevensis (Pierre ex Pit.) Neupane & N. Wikstrom	China: Xiwen Li 59-13549 (KUN)	KP994258	KR005743	KR005803	/	/
Involucrella coronaria (Kurz) Neupane & N.Wikstrom	China: Xing Guo & Ping Yang 22-1 (IBSC)	JX111218	JX111104	JX111270	JX111177	JX111344
Leptopetalum biflorum (L.) Neupane & N. Wikstrom	Singapore: Ruijiang Wang SIN03 (IBSC)	JX111238	JX111120	JX111302	JX111192	JX111376
Leptopetalum pteritum (Blume) Neupane & N. Wikstrom	China: Ruijiang Wang 1478 (IBSC)	JF699944	JF700094	/	JF699799	/
Oldenlandia capensis L. f. var. *capensis*	Zambia: Dessein et al. 843 (BR)	AM939496	EU557737	EU543048	/	EU543133
Oldenlandia corymbosa L. var. *corymbosa*	Singapore: Ruijiang Wang SIN02 (IBSC)	JX111239	JX111121	JX111306	JX111194	JX111380
Oldenlandia duemmeri S. Moore	Uganda: W. H. Lewis 6018 (GH)	HE657744	HE657629	HE649881	/	/
Oldenlandia umbellata L.	Sri Lanka: F. Fagerlind 3320 (S)	HE657674	HE657569	/	/	/
Oldenlandia wiedemannii K. Schum.	Kenya: Luke & Luke 8362 (UPS)	AM939525	EU557756	EU543063	/	EU543151
Parainvolucrella scabra (Wall. ex Kurz) M.D. Yuan & R.J. Wang	China: Mingdeng Yuan & Yida Xu YS398_1 (IBSC)					
Parainvolucrella scabra (Wall. ex	China: Mingdeng Yuan & Yida					

Kurz) M.D. Yuan & R.J. Wang	Xu YS398_2 (IBSC)					
Parainvolucrella scabra (Wall. ex Kurz) M.D. Yuan & R.J. Wang	China: Mingdeng Yuan & Yida Xu YS399 (IBSC)					
Parainvolucrella scabra (Wall. ex Kurz) M.D. Yuan & R.J. Wang	Thailand: Neupane 183 (ODU)	KP994264	KR005751	KR005812	/	/
Paraknoxia parviflora (Stapf ex Verdc.) Bremek.	Zambia: Dessein et al. 678 (BR)	AM267020	EU557757	EU543064	/	EU543152
Scleromitrion angustifolium (Cham. & Schltdl.) Benth.	China: Xing Guo et al. 12 (IBSC)	JF976506	JF700108	JX111297	JF699810	JX111370
Scleromitrion diffusum (Willd.) R.J. Wang	China: Xing Guo 51 (IBSC)	JF699932	JF700081	JX111308	JF699789	JX111381
Scleromitrion koanum (R.J. Wang) R.J. Wang	China: Ruijiang Wang et al. 978 (IBSC)	JX111215	JX111101	JX111267	JX111174	JX111341
Scleromitrion pinifolium (Wall. ex G. Don) R.J. Wang	China: Ruijiang Wang 1231 (IBSC)	JX111240	JF700094	JX111311	JX111196	JX111384

Figure 1. *Parainvolucrella scabra*: **A** habit **B** inflorescences **C** leaf adaxial surface **D** leaf abaxial surface **E** stem and its transverse section **F**–**H** long-styled flower **I**–**K** short-styled flower **L** young capsule **M** mature capsules **N** seeds.

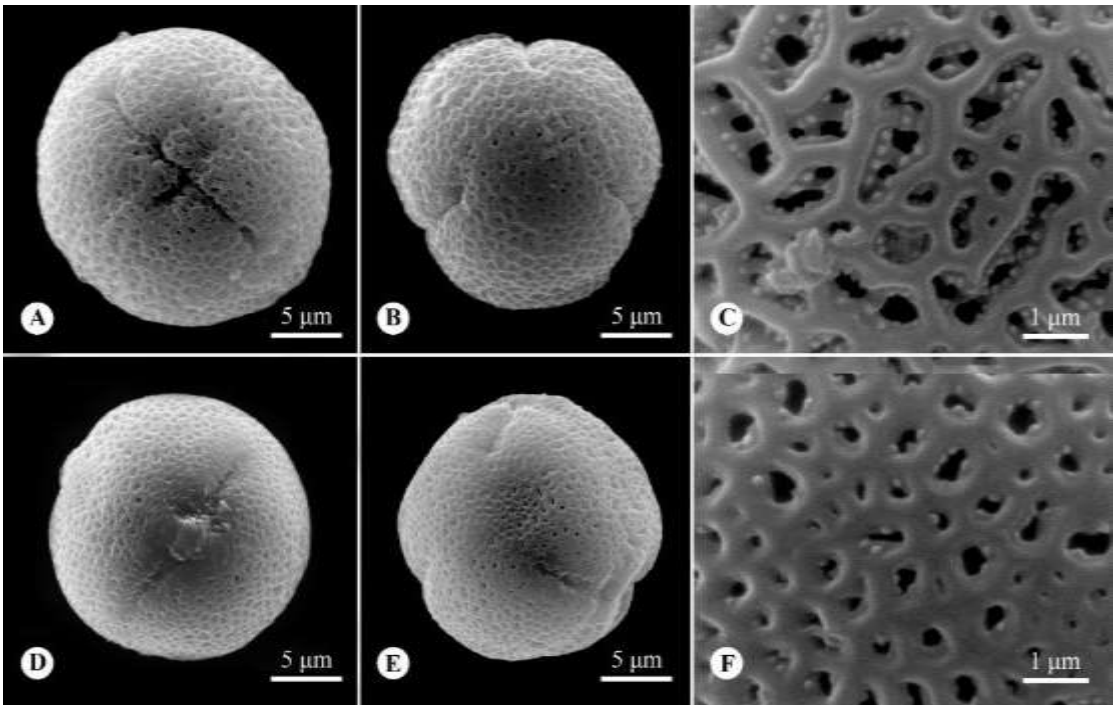

Figure 2. Pollen morphology of *Parainvolucrella scabra* under SEM: **A, D** equatorial view **B, E** polar view **C, F** reticulate ornamentation.

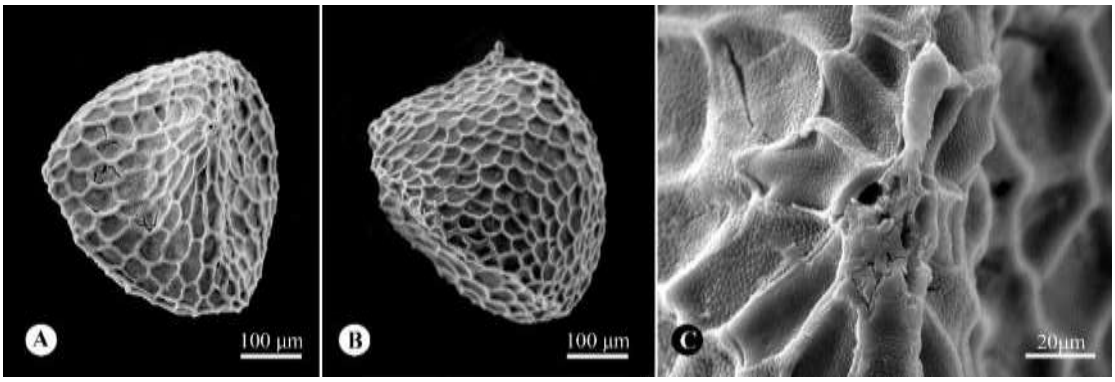

Figure 3. Seed morphology of *Parainvolucrella scabra*: **A** ventral side **B** dorsal side **C** seed surface ornamentations.

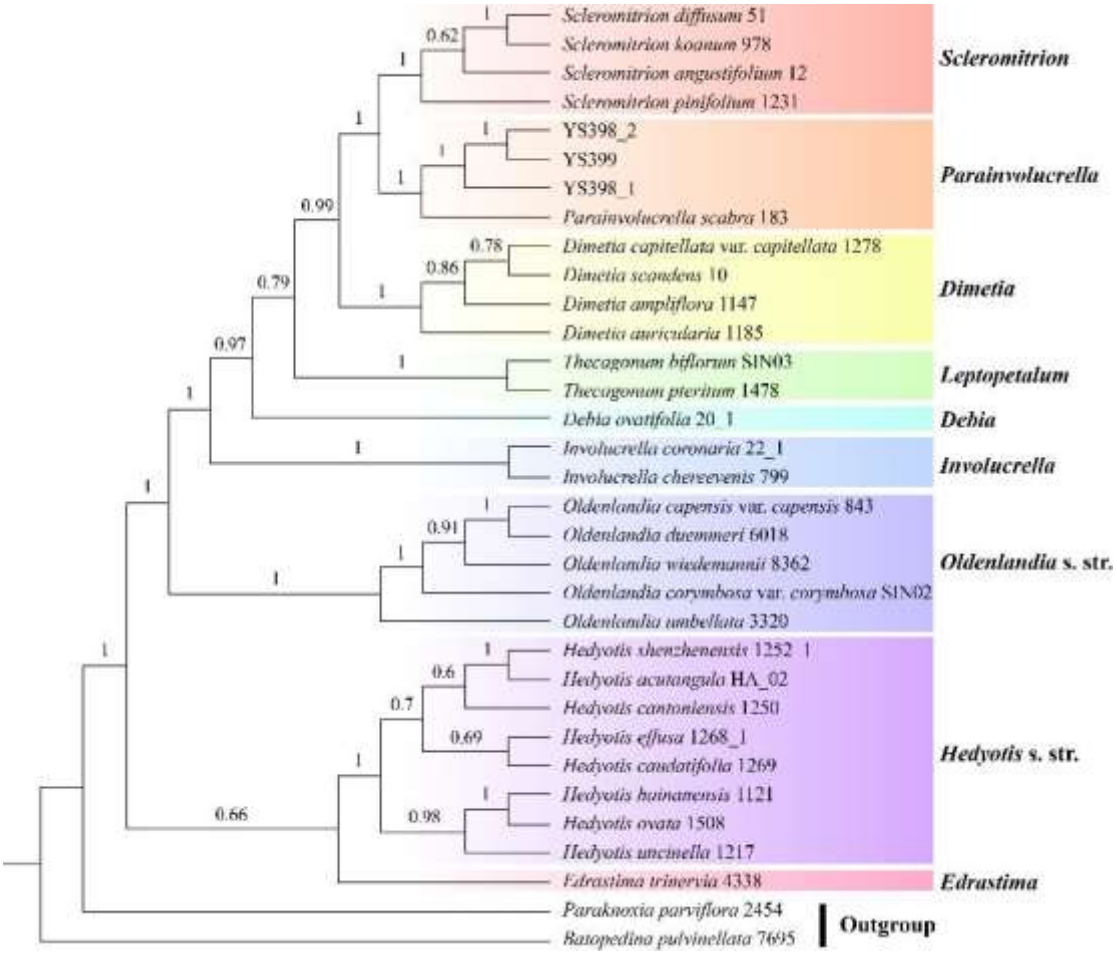

Figure 4. Bayes 50% major rule consensus tree derived from a combined analysis of ITS and plastid *pet*D, *rps*16, *trn*H-*psb*A and *trn*L-F, posterior probability (PP) are indicated above branches.