Studies of the pollen morphology and taxonomy of the tribes Loteae and Coronilleae (Papilionoideae; Leguminoseae). 3, Coronilla L. and related genera and systematic conclusions

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Abstract

The pollen morphology of 48 taxa has been studied with light and electron microscopy. The pollen is three-zonocolporate, elliptical or more or less rectangular, sometimes circular, in equatorial outline and circular or triangular in polar outline; small or medium size, \( P \times E = (14-30) \times (9-26) \ \mu m \). The colpi are long, the endoapertures elongate. The ornamentation is perforate, microreticulate, granulate-verrucate, striate-rugulate perforate-granulate or finely granular. Exine is 0.5-2 \( \mu m \) thick at the mesocolpium. The endexine thickened at the equator, thinner at the poles, the foot layer very thin or absent, the infratectum columellate; the columellae are sometimes almost granular often widely spaced with expanded bases and the tectum thick. Ornamentation is the primary basis for the division into types.

Five pollen types are recognised. With the exception of Securigera, which has similar pollen to Coronilla, the types correspond well with the genera recognised in the group. The pollen morphology of Scorpiurus is distinct from that of the rest of the group.

Pollen morphology is discussed in relation to the taxonomy of the group and its significance to relationships and evolution of the tribes is considered.

It is concluded that there is little evidence from pollen morphological studies to support the separation of the Coronilleae and Loteae as two tribes. It is suggested that the group Loteae shows some affinities in pollen morphology with tropical tribes as for example Phaseoleae as well as with temperate herbaceous tribes.

1. Introduction

Coronilla and related genera comprising the tribe Coronilleae as circumscribed by Polhill (1981) has about 50 species primarily centred around the Mediterranean, extending to the Atlantic Islands, Western Asia and Northeast Africa. The monotypic genus Antopetitia A. Richard occurs in tropical Africa.

As discussed earlier (Diez and Ferguson, 1991,1994) the delimitation of the tribes Loteae and Coronilleae and the generic limits within the tribes has long been problematic, various authors adopting different limits. Polhill (1981) reviews the problems separating Coronilleae from Loteae by the jointed fruits but admits that there is no real practical reason why the two tribes should not be

Some recent authors including Ball (1968) and Chamberlain (1970) have treated *Securigera* de Candolle as a monotypic genus while others including Meikle (1977) and Schmidt (1978),(1979) have included *Securigera securidaca* in *Coronilla*. Lassen (1989a) redefined the limits of the two genera recognising nine species in *Coronilla* and twelve species in *Securigera*. He clearly distinguishes these genera from *Hippocrepis* Linnaeus. At about the same time Lassen (1989b) transferred *Coronilla emerus* to *Hippocrepis*. This species had hitherto been retained in *Coronilla* by most authors including Ball (1968), Chamberlain (1970) and Meikle (1977).

Dominguez and Galiano (1974b) in revising the morphologically specialised *Scorpiurus* Linnaeus separate four species, however, most authors including Ball (1968) and Greuter et al. (1989) recognised only two.

*Hammatolobium* Fenzl, the remaining genus placed in Coronilleae by Polhill (1981) has been transferred to *Tripodium* Medicus and redefined by Lassen (1986) and this treatment is followed by Greuter et al. (1989). The pollen morphology of this genus is described and discussed by Diez and Ferguson (1991).

The pollen morphology of the *Coronilla* group has been studied by a number of workers especially of the species in the Iberian Peninsula. Ohashi (1971) examined the pollen of ten species in light microscopy including *Antopetitia* which he suggests is palynologically similar to *Ornithopus*. Pire (1974) included a number of species in the group in a study of the pollen of the tribe Hedysareae while Dominguez and Galiano (1974a) examined the pollen of *Scorpiurus*. The pollen of eleven of the annual species of *Hippocrepis* were investigated by Dominguez (1976). Ferguson and Skvarla (1981) as a part of a review of the pollen morphology of the subfamily Papilionoideae illustrate the pollen of *Scorpiurus villosa* with scanning and transmission electron microscopy and go on to suggest that in the tribe Coronilleae there is a little variation in the tectum which may prove to have some taxonomic significance at generic level but the apertures are unspecialised.

The pollen of four species of *Ornithopus* was examined by Alsina Aser (1984) using light and scanning electron microscopy. Prados et al. (1985a),Prados et al. (1985b) studied the pollen of some eleven species from *Coronilla, Hippocrepis, Ornithopus* and *Scorpiurus*. They included these data in a numerical analysis, however, the results do not clarify relationships greatly.

Fernández (1987) has examined pollen of four species of *Coronilla* and placed these in a type of their own distinguished by rugulate ornamentation from the pollen of three species of *Ornithopus*. The latter are placed in a separate type with rectangular shaped pollen that is smooth at the poles and verrucate at the equator. She also investigated the pollen of five species of *Hippocrepis* and three species of *Scorpiurus* which she placed in a large and not well defined pollen type including species of *Trifolium* Linnaeus, *Medicago* Linnaeus and *Anthyllis* Linnaeus.

Recently, Crompton and Grant (1993) in an extensive review and numerical analysis of the pollen morphology of the genus *Lotus* concluded that the Old World species had less variable pollen than the New World taxa. They suggest that the pollen sculpturing pattern of some members of the Coronilleae differ from Loteae and described *Ornithopus* as having verrucate clusters with nanoprocesses, *Scorpiurus* as reticulate and *Hippocrepis* slightly reticulate. They do not describe the pollen of *Coronilla*.

The purpose of this paper, the last of a series (see also Diez and Ferguson, 1991, 1994) is to describe the pollen morphology of *Coronilla* and related genera and to see how much palynological characters can contribute to the understanding of relationships between the tribes Loteae and Coronilleae.

### 2. Material and methods

Pollen material was obtained from the Herbarium, Department of Botany, Faculty of Biology, University of Sevilla (SEV) and the Herbarium, Royal Botanic Gardens, Kew (K). Details of the specimens examined are given below.
Pollen was acetolysed in the standard way (Erdtman, 1960). For light microscopy (LM) slides were prepared by mounting the pollen in glycerol jelly. Twenty to thirty measurements of pollen grains (P and E) were made from each specimen.

The measurements shown in Table 1 represent the mean and range of all the samples examined of each taxon. Fewer (approximately five) measurements were made of the other characters.

For scanning electron microscopy (SEM) pollen was air dried on specimen stubs from 95% ethanol and examined with a Jeol T100 or a Hitachi 2400 SEM. For transmission electron microscopy (TEM) acetolysed exines were fixed with 2% osmium tetroxide, pre-stained with uranyl acetate and embedded in epon-araldite (Skvarla, 1966; Skvarla and Pyle, 1968). Sections were cut with a diamond knife and post-stained with uranyl acetate and Reynold's lead citrate using an LKB Ultrastainer and examined with a Hitachi H300 TEM.

For transmission electron microscopy (TEM) acetolysed exines were fixed with 2% osmium tetroxide, pre-stained with uranyl acetate and embedded in epon-araldite (Skvarla, 1966; Skvarla and Pyle, 1968). Sections were cut with a diamond knife and post-stained with uranyl acetate and Reynold's lead citrate using an LKB Ultrastainer and examined with a Hitachi H300 TEM.

The nomenclature used for the European species generally follows Tutin et al. (1968) but the most recent changes proposed by Lassen (1986), (1989a), (1989b) and Greuter et al. (1989) are adopted and these changes are shown in the list of specimens examined. For any African or Asian species not included in Lassen (1989a) the nomenclature used by Lock (1989) and Lock and Simpson (1991) is followed. The terminology in general follows Fægri and Iversen (1975) and Punt et al. (1994).

3. Specimens investigated

*Antopetitia abyssinica* (L.) A. Richard. Nigeria, Daramola 6230 (K); Tanzania, Staples, 373 (K); Stolz, 207 (K)

*Coronilla coronata* L. Italy, Feoli Chiapella (SEV 75720)

*Coronilla juncea* L. Portugal, Béliz and Guerra (SEV 12791); Spain, Aparicio (SEV 56786); Galiano et al. (SEV 119620); L. Portugal, Béliz and Guerra (SEV 12791); L. Spain, Loidi (SEV 101058) and Greuter et al. (1989a) and Greuter et al. (1989b) and Greuter et al. (1989) are adopted and these changes are shown in the list of specimens examined. For any African or Asian species not included in Lassen (1989a) the nomenclature used by Lock (1989) and Lock and Simpson (1991) is followed. The terminology in general follows Fægri and Iversen (1975) and Punt et al. (1994).

*Coronilla scorpioides* (L.) Koch. Spain, Galiano et al. (SEV 7935); Casaseca (SEV 3194); Domínguez and Gibbs (SEV 16313)

*Coronilla valentina* L.

subsp. *glauc*a (L.) Battandier (= *C. glauca* L.). Spain, Andrés and Arroyo (SEV 87111); Mayor (SEV 24994)

subsp. *pentaphylla* (Desfontaines) Battandier. Algeria, Balansa 380 (K) Coronilla viminalis Salisbury. Morocco, Trethewy 227 (K)

*Hippocrepis areolata* Desvauex (= *H. bicontorta* Loiselieur-Deslongchamps). Qatar, Wilcox 106 (K); Saudi Arabia, Collette 2496 (K)

*Hippocrepis atlantica* Ball. Morocco, Ball s.n. (K)

*Hippocrepis biflora* Sprengel (= *H. unisiliquosa* L. subsp. biflora (Sprengel) Bolös and Vigo). Spain, Galiano and Domínguez (SEV 15138); Yugoslav, Prior, s/n (K)

*Hippocrepis brevipetala* (Murbeck) Domínguez. Algeria, Birch and Wolfe s.n. (K); Morocco, Blanché et al. (SEV 125355)

*Hippocrepis ciliata* Willdenow. Spain, Galiano and Domínguez (SEV 13909); Peris and Stubing (SEV 121097)

*Hippocrepis commutata* Pau. Spain, Ladero and Fuertes (SEV 93129); Nieto Feliner (SEV 123477)

*Hippocrepis comosa* L. Spain, Loidi (SEV 101058)

*Hippocrepis constricta* G. Kunze (= *H. multisiliquosa* L. subsp. constricta (Kunze) Maire). Saudi Arabia, Collette 740 (K)

*Hippocrepis cyclocarpa* Murbeck. Egypt, Palmer 69 (K)

*Hippocrepis emerus* (L.) Lassen (= *Coronilla emerus* L.)

subsp. *emeroides* (Boissier and Spruner) Lasset (= *Coronilla emeroides* Boissier and Spruner; *C. emerus* L. subsp. *emeroides* Holmboe). Russia, Chechrstakov (SEV 43352)

subsp. *emer* (= *Coronilla emerus* L.). Italy, Chiapella (SEV 75721)

*Hippocrepis eriocarpa* (Boissier) Boissier (= *Hippocrepis squamata* (Cavanilles) Cosson subsp. *eriocarpa* (Boissier) Nyman). Spain, Castroviejo (SEV 125155)

*Hippocrepis glauca* Tenore (= *H. comosa* L. subsp. *glauca* (Tenore) Bonnier and Layens). Spain, Fernández (SEV 25471)

*Hippocrepis minor* Munby. Algeria, Birch and Wolfe s.n. (K)

*Hippocrepis multisiliquosa* L. Spain, Cabezudo, Domínguez and Talavera (SEV 7831)

*Hippocrepis neglecta* Lassen. Morocco, Balls 13 2456 (K)

*Hippocrepis salzmannii* Boissier and Reuter. Spain, Luque, Talavera and Valdés (SEV 11079)

*Hippocrepis scabra* de Candolle (≈ *H. comosa* L. subsp. *scabra* (de Candolle) Bolös and Vigo). Spain, Martínez (SEV 120619)

*Hippocrepis squamata* (Cavanilles) Cosson (= *H. comosa* L. subsp. *squamata* (Cavanilles) Bolös and Vigo). Spain, Charpin and Deferrand (SEV 91954); Asensi and Diez (SEV 108523)

*Hippocrepis unisiliquosa* L.

subsp. *bislíqu* (Forsskal) Bornmüler (≈ *H. bislíqu* Forsskal). Iraq, Rami and Rechinger 17721 (K)

subsp. *unisiliquosa*. Jordan, Simpson 53249 (K)

*Hippocrepis valentina* Boissier (≈ *H. balearica* Jacquin subsp. *valentina* (Boissier) Uhová). Spain, Stibbing (SEV 110926)

*Ornithopus compressus* L. Spain, Diez, Pastor and Silvestre (SEV 73178)
Table 1

Showing taxa examined arranged in pollen types, with ornamentation, measurements (μm) of the mean and ranges for the polar (P) and equatorial (E) axes and the shape index P/E.

<table>
<thead>
<tr>
<th>Types and taxa</th>
<th>Ornamentation</th>
<th>Polar axis</th>
<th>Equatorial axis</th>
<th>P/E</th>
</tr>
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<tr>
<td><strong>Type I</strong></td>
<td></td>
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<tr>
<td><em>Coronilla coronata</em></td>
<td>striate-rugulate</td>
<td>19 (20.35) 22</td>
<td>15 (16.25) 18</td>
<td>1.11 (1.25) 1.31</td>
</tr>
<tr>
<td><em>C. juncea</em></td>
<td>striate-rugulate</td>
<td>15 (18.27) 21</td>
<td>10 (14.37) 18</td>
<td>1.06 (1.27) 1.66</td>
</tr>
<tr>
<td><em>C. minima</em></td>
<td>striate-rugulate</td>
<td>17 (19.35) 22</td>
<td>15 (16.05) 18</td>
<td>1.05 (1.20) 1.37</td>
</tr>
<tr>
<td><em>C. ramosissima</em></td>
<td>striate-rugulate</td>
<td>17 (19.25) 21</td>
<td>13 (14.87) 16</td>
<td>1.18 (1.29) 1.40</td>
</tr>
<tr>
<td><em>C. repanda</em> subsp. <em>dura</em></td>
<td>striate-rugulate</td>
<td>14 (18.10) 21</td>
<td>10 (13.39) 16</td>
<td>1.13 (1.35) 1.80</td>
</tr>
<tr>
<td><em>C. scorpioides</em></td>
<td>striate-rugulate</td>
<td>15 (17.20) 20</td>
<td>9 (12.16) 14</td>
<td>1.14 (1.41) 1.72</td>
</tr>
<tr>
<td><em>C. valentina</em> subsp. <em>glaucía</em></td>
<td>striate-rugulate</td>
<td>19 (22.50) 24</td>
<td>14 (16.92) 22</td>
<td>1.00 (1.28) 1.56</td>
</tr>
<tr>
<td><em>C. viminalis</em></td>
<td>striate-rugulate</td>
<td>23 (25.60) 29</td>
<td>18 (19.40) 21</td>
<td>1.20 (1.31) 1.44</td>
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<td><em>Securigera atlantica</em></td>
<td>striate-rugulate</td>
<td>23 (24.45) 26</td>
<td>18 (19.80) 21</td>
<td>1.14 (1.23) 1.33</td>
</tr>
<tr>
<td><em>S. cretica</em></td>
<td>striate-rugulate</td>
<td>20 (22.37) 25</td>
<td>17 (18.70) 20</td>
<td>1.00 (1.23) 1.41</td>
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<tr>
<td><em>S. elegans</em></td>
<td>striate-rugulate</td>
<td>23 (25.15) 28</td>
<td>20 (21.50) 23</td>
<td>1.08 (1.16) 1.27</td>
</tr>
<tr>
<td><em>S. grandiflora</em></td>
<td>striate-rugulate</td>
<td>24 (24.35) 26</td>
<td>19 (19.35) 20</td>
<td>1.20 (1.25) 1.31</td>
</tr>
<tr>
<td><em>S. orientalis</em></td>
<td>striate-rugulate</td>
<td>20 (22.83) 25</td>
<td>16 (17.18) 18</td>
<td>1.22 (1.32) 1.50</td>
</tr>
<tr>
<td><em>S. parviflora</em></td>
<td>striate-rugulate</td>
<td>21 (22.15) 23</td>
<td>17 (18.35) 19</td>
<td>1.15 (1.20) 1.29</td>
</tr>
<tr>
<td><em>S. securidaca</em></td>
<td>striate-rugulate</td>
<td>20 (23.00) 26</td>
<td>18 (19.62) 22</td>
<td>1.09 (1.17) 1.30</td>
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<tr>
<td><em>S. varia</em></td>
<td>striate-rugulate</td>
<td>23 (26.45) 29</td>
<td>17 (22.30) 25</td>
<td>1.04 (1.18) 1.47</td>
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<td><strong>Type II</strong></td>
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<td><em>Ornithopus compressus</em></td>
<td>granulate-verrucate</td>
<td>23 (23.80) 25</td>
<td>19 (19.60) 21</td>
<td>1.15 (1.21) 1.31</td>
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<tr>
<td><em>O. isthmocarpus</em></td>
<td>granulate-verrucate</td>
<td>25 (28.25) 30</td>
<td>21 (23.37) 25</td>
<td>1.12 (1.20) 1.30</td>
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<tr>
<td><em>O. perpusillus</em></td>
<td>granulate-verrucate</td>
<td>18 (20.25) 22</td>
<td>13 (15.55) 18</td>
<td>1.01 (1.30) 1.46</td>
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<tr>
<td><em>O. pinnatus</em></td>
<td>granulate-verrucate</td>
<td>25 (28.52) 28</td>
<td>17 (19.52) 22</td>
<td>1.09 (1.32) 1.58</td>
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<tr>
<td><em>O. sativus</em></td>
<td>granulate-verrucate</td>
<td>22 (25.62) 28</td>
<td>20 (21.72) 24</td>
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<td><em>O. uncinatus</em></td>
<td>granulate-verrucate</td>
<td>23 (24.30) 26</td>
<td>17 (18.85) 23</td>
<td>1.08 (1.28) 1.46</td>
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<tr>
<td><strong>Type III</strong></td>
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<td>perforate</td>
<td>15 (18.17) 22</td>
<td>13 (14.41) 17</td>
<td>1.06 (1.26) 1.46</td>
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<tr>
<td><em>H. biflora</em></td>
<td>perforate</td>
<td>21 (21.89) 25</td>
<td>15 (17.74) 20</td>
<td>1.05 (1.23) 1.66</td>
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<tr>
<td><em>H. ciliata</em></td>
<td>perforate</td>
<td>16 (18.62) 20</td>
<td>13 (14.47) 16</td>
<td>1.14 (1.28) 1.42</td>
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<td><em>H. commutata</em></td>
<td>perforate</td>
<td>16 (18.95) 22</td>
<td>12 (14.82) 20</td>
<td>1.00 (1.27) 1.66</td>
</tr>
<tr>
<td><em>H. comosa</em></td>
<td>perforate</td>
<td>18 (19.00) 20</td>
<td>14 (14.70) 16</td>
<td>1.20 (1.29) 1.42</td>
</tr>
<tr>
<td><em>H. constricta</em></td>
<td>perforate</td>
<td>15 (15.85) 17</td>
<td>14 (14.60) 16</td>
<td>1.00 (1.08) 1.21</td>
</tr>
<tr>
<td><em>H. cyclocarpa</em></td>
<td>perforate</td>
<td>16 (17.50) 19</td>
<td>13 (14.30) 16</td>
<td>1.12 (1.22) 1.38</td>
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<td><em>H. emerus</em> subsp. <em>emeroides</em></td>
<td>perforate</td>
<td>19 (23.15) 27</td>
<td>20 (23.30) 26</td>
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<td><em>subsp. emerus</em></td>
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<td>0.95 (1.09) 1.25</td>
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<td>15 (16.90) 19</td>
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<td>15 (16.60) 18</td>
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<td><em>H. minor</em></td>
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<td>14 (15.25) 16</td>
<td>1.25 (1.31) 1.46</td>
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<td><em>H. neglecta</em></td>
<td>perforate</td>
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<td>14 (15.15) 16</td>
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<td><em>H. salzmanni</em></td>
<td>perforate</td>
<td>22 (23.75) 25</td>
<td>18 (18.35) 20</td>
<td>1.21 (1.29) 1.38</td>
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<td><em>H. scabra</em></td>
<td>perforate</td>
<td>21 (22.05) 24</td>
<td>16 (18.05) 19</td>
<td>1.10 (1.22) 1.33</td>
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<td><em>H. squamata</em></td>
<td>perforate</td>
<td>20 (22.82) 28</td>
<td>16 (17.92) 21</td>
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<td><em>H. unisiliquosa</em></td>
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<td>15 (16.00) 17</td>
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<td>13 (14.70) 15</td>
<td>1.26 (1.40) 1.53</td>
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<td>18 (20.60) 23</td>
<td>15 (17.00) 18</td>
<td>1.10 (1.20) 1.35</td>
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Table 1 (continued)

<table>
<thead>
<tr>
<th>Types and taxa</th>
<th>Ornamentation</th>
<th>Polar axis</th>
<th>Equatorial axis</th>
<th>P/E</th>
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<td><strong>Subtype IIIb</strong></td>
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<td>H. atlantica</td>
<td>perforate–rugulate</td>
<td>18 (20.05)</td>
<td>16 (17.15)</td>
<td>21</td>
</tr>
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<td>H. brevipetala</td>
<td>perforate–rugulate</td>
<td>17 (19.42)</td>
<td>14 (14.95)</td>
<td>22</td>
</tr>
<tr>
<td>H. multisiliquosa</td>
<td>perforate–rugulate</td>
<td>20 (22.65)</td>
<td>15 (17.15)</td>
<td>25</td>
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<td><strong>Type IV</strong></td>
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<tr>
<td>Antopotetia abyssinica</td>
<td>finely granular</td>
<td>20 (23.35)</td>
<td>21 (23.45)</td>
<td>26</td>
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<td><strong>Type V</strong></td>
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<td></td>
</tr>
<tr>
<td>Scorpiurus muricatus</td>
<td>microreticulate</td>
<td>18 (21.60)</td>
<td>12 (13.85)</td>
<td>24</td>
</tr>
<tr>
<td>S. vermiculatus</td>
<td>microreticulate</td>
<td>20 (22.47)</td>
<td>13 (14.05)</td>
<td>25</td>
</tr>
</tbody>
</table>

Ornithopus isthmocarpus Cosson (=Ornithopus sativus Brotero subsp. isthmocarpus (Cosson) Dostfil). Morocco, Trethwey, 21 (K); Trethwey, 230 (K).

Ornithopus perpusillus L. England, Milne-Redhead, 5990 (K); Spain, Diez, Pastor and Silvestre (SEV 73178).

Ornithopus pinnatus (Miller) Druce. Spain, Segura Subizarreta (SEV 41058); Segura Subizarreta (SEV 38659).

Ornithopus sativus Brotero (=O. sativus Brotero subsp. roseus (Dufour) Dostfil). Spain, Cabezudo (SEV 21937); Cabezudo (SEV 80376).

Ornithopus uncinatus Maire and Samuelsson. Morocco, Samuelsson 7239 (K).

Securigera atlantica Boissier and Reuter (=Coronilla atlantica (Boissier and Reuter) Boissier). Algeria, Durando 521 (K).

Securigera cretica (L.) Lassen (=Coronilla cretica L.). Greece, Atchley 1639 (K); Yugoslavia, Huser s.n. (K).

Securigera elegans (Pancic) Lassen (=Coronilla elegans Pancic). Greece, Alston and Sandwith 988 (K).

Securigera grandiflora Lassen (=Coronilla grandiflora Boissier). Turkey, Kotsch 48 (K). Securigera orientalis (Miller) Lassen (=Coronilla orientalis Miller; Coronilla orientalis var. balansae Boissier). Turkey, Balls 13413 (K); Stainton 8193 (K); Stainton and Henderson 5934 (K).

Securigera parviflora (Desvaux) Lassen (=Coronilla rostrata Boissier and Spruner; C. parviflora Willdenow; Artrolobium parviflorum Desvaux). Greece, Reverchon 38 (K).

Securigera securidaca (L.) Degen (=Coronilla securidaca L.; Securigera coronilla de Candolle; Bonaveria securidaca (L.) Halácsy). Greece, Shay 80/85 (K).

Securigera varia (L.) Lassen (=Coronilla varia L.). France, Tarascon and Ledoux (SEV 22540); Switzerland, Wyatt, 31 (K).

4. Results

The pollen of Coronilla and related genera is generally three-zonocolporate, small in size, about 20–25 μm, with endoapertures lalongate and with exine stratification comprised of a thick endexine at the mesocolpium, foot layer thin or absent, an infratectum with short usually broad columellae, or sometimes more or less granular and a thick complete tectum.

4.1. Type I (Plate I, 1–15)

Elliptical or rectangular–elliptical in equatorial outline and more or less circular or triangular–circular in polar outline. Spheroidal to prolate, P/E = 1.00–1.80. Small to medium size, P × E = (14–29) × (9–25) μm. Colpi terminal, costate, membrane granular; endoapertures lalongate, more or less rectangular or elliptical in outline, constricted or nonconstricted in the middle, sometimes X-shaped, (2–6) × (5–14) μm. Exine 1–1.5 μm thick at the mesocolpium, with a thick endexine, more reduced at the poles, foot layer absent, short and widely spaced columellae and thick tectum. Ornamentation striate–rugulate.

The pollen of Securigera is a little larger than Coronilla, with the exception of C. viminalis, where the pollen size is similar to that of Securigera.

The ornamentation, outline in equatorial view and exine thickness varies. Five pollen types and two subtypes are recognised:

1a. Ornamentation striate-rugulate ................................................................................................................................. Type I
b. Ornamentation not striate-rugulate ......................................................................................................................... 2

2a. Ornamentation finely reticulate .................................................................................................................................. Type V
b. Ornamentation perforate, perforate-rugulate, granulate-verrucate or perforate finely granulate-rugulate ............................................................................................................................................................ 3

3a. Pollen with ornamentation granulate-verrucate and rectangular in equatorial outline .................................................................................................................................................................................. Type II
b. Pollen with ornamentation perforate, perforate-rugulate or perforate finely granulate-rugulate and circular, elliptical or rectangular-elliptical in equatorial outline .................................................................................................................................................................................. 4

4a. Pollen with perforate–finely granulate-rugulate ornamentation, more or less circular in equatorial outline and exine 1.5–2 μm thick at mesocolpium ................................................................................ Type IV
b. Pollen with perforate or perforate-rugulate ornamentation, elliptical or rectangular-elliptical in equatorial outline and exine 0.5–1.5 μm thick at mesocolpium ......................................................... Type III (5)

5a. Ornamentation perforate .............................................................................................................................................. Subtype IIIa
b. Ornamentation perforate–rugulate ............................................................................................................................ Subtype IIIb

The taxa examined are arranged in pollen types with measurements in microns of the mean and ranges for the polar (P) and equatorial (E) axes, the shape index P/E and the ornamentation are shown in Table 1.

4.2. Type II (Plate II, 16–26)

Rectangular in equatorial outline and more or less triangular–angulaperturate in polar outline. Spheroidal to prolate, $P/E = 1.00–1.58$. Small to medium size, $P \times E = (18–30) \times (17–25)$ μm. Colpi more or less terminal, costate, membrane granular; endoapertures lalongate, more or less elliptical in outline and constricted in the middle, $(2–5) \times (4–11)$ μm. Exine 1–2 μm thick at the meso-
colpium, with a thick endexine, very reduced at the poles, foot layer absent, short, widely spaced irregular columellae, sometimes almost granular like and thick tectum. Ornamentation granulate–verrucate and perforate at the mesocolpium and more or less psilate at the apocolpia.

The endoapertures in *Ornithopus perpusillus* are a little smaller, (2–3) × (4–6) μm. typical of Type II.

Taxa included: *Ornithopus compressus*, *O. isthmocarpus*, *O. perpusillus*, *O. pinnatus*, *O. sativus*, *O. uncinatus*.

4.3. Type III (Plate III, 27–37)

Elliptical or rectangular–elliptical in equatorial outline and more or less circular or triangular–circular in polar outline. Oblate–spheroidal to prolate, \( P/E = 0.87–1.66 \). Small to medium size, \( P \times E = (15–28) \times (12–26) \) μm. Colpi more or less terminal, costate, membrane granular; endoapertures lalongate, elliptical or more or less rectangular in outline, slightly constricted or nonconstricted, sometimes circular in *Hippocrepis unisiliquosa* subsp. *unisiliquosa*, (3–5) × (5–11) μm. Exine 0.5–1.5 μm thick at the mesocolpium, with a thick endexine, very reduced at the poles, foot layer very reduced, columellae quite dense, short, broad, and thick tectum.

Two subtypes can be distinguished by ornamentation:

4.3.1. Subtype IIIa (Plate III, 27–32, 35–37)

Ornamentation perforate.

The pollen of *Hippocrepis consticta* and *H. unisiliquosa* subsp. *bisiliqua* is a little smaller in size, about 16 μm. In the rest of the species the pollen is 20 μm or more in size. The exine is a little less thick in *H. bicornorta*, 0.5–1 μm, and the endoapertures are smaller in *H. bicornorta* and *H. comosa*.


4.3.2. Subtype IIIb (Plate III, 33–34)

Ornamentation perforate–rugulate on the mesocolpium with some more or less distinct muri.

There is a some similarity between the ornamentation of this subtype and that of Type I.

Taxa included: *Hippocrepis atlantica*, *H. brevipetala*, *H. multisilquosa*.

4.4. Type IV (Plate IV, 38–46)

More or less circular or slightly elliptical in equatorial outline and circular in polar outline. Spheroidal, \( P/E = 0.86–1.09 \). Small to medium size,
(for description see p. 250)
(for description see p. 250)
$P \times E = (20–26) \times (21–26) \mu m$. Colpi more or less terminal, costate, membrane granular; endoapertures lalongate, elliptical or more or less rectangular in outline, slightly constricted or nonconstricted (7–10) × (10–12) \mu m. Exine 1.5–2 \mu m thick at the mesocolpium with a thick endexine, reduced at the poles, foot layer thin, columellae short, irregular sometimes more or less granular, widely spaced, broad, expanded at base and fusing to form a foot layer and thick tectum. Ornamentation perforate, finely granular–rugulate at the mesocolpium and more or less psilate at the apocolpium.

Taxa included: *Antopetitia abyssinica*.

4.5. Type V (Plate IV, 47–54)

Elliptical or rectangular–elliptical in equatorial outline and more or less circular in polar outline.

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**PLATE III (see p. 248)**

In 27–31 and 35 scale bar equals 5 \mu m; in 32–34 and 36 scale bar equals 2 \mu m; in 37 scale bar equals 1 \mu m.

27–37. Type III. 27–32 and 35–37 Subtype IIIa

27. *Hippocrepis biflora* (SEV 22668), LM equatorial view.


31, 32. *Hippocrepis glauca* (SEV 25471).

31. SEM equatorial view.

32. SEM details of ornamentation and aperture.


33. SEM details of ornamentation.

34. SEM Details of ornamentation and aperture.

35–37. *Hippocrepis biflora* (Prior, s.n.).

35. TEM polar section through whole pollen grain.

36. TEM exine stratification at polar area.

37. TEM exine stratification at mesocolpium.

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**PLATE IV (see p. 249)**

In 38–42, 44 and 47–51 scale bar equals 5 \mu m; in 43, 45, 46 and 52–54 scale bar equals 2 \mu m.

38–46. Type IV. *Antopetitia abyssinica* (38–41 and 43, Daramola, 6230; 42, Stolz, 207; 44–46, Staples, 373).

38. LM equatorial view.

39. LM equatorial view.

40. LM endoaperture.

41. LM polar view.

42. SEM equatorial view.

43. SEM detail of ornamentation.

44. TEM polar section through whole pollen grain.

45. TEM exine stratification at polar area.

46. TEM exine stratification at apertural area.


49. *Scorpiurus vermiculatus* (SEV 46669), LM endoaperture.

50. *Scorpiurus maricatus* (SEV 7956), LM polar view.

51, 52. *Scorpiurus maricatus* (Atchley, s.n.).

51. SEM equatorial view.

52. SEM detail of ornamentation.


53. TEM exine stratification at apertural area.

54. TEM exine stratification at mesocolpium.
Prolate-spheroidal to prolate, \( P/E = 1.12-1.76 \). Small to medium size, \( P \times E = (18-25) \times (12-16) \) \( \mu m \). Colpi terminal, costate, membrane granular; endoapertures lalongate, more or less elliptical in outline, slightly constricted or nonconstricted, \((2.5-3) \times (3-6) \) \( \mu m \). Exine ca. 1 \( \mu m \) thick at the mesocolpium, with a thick endexine, more reduced at the poles, foot layer absent, columellae short, comparatively thin, regular and dense, a little more widely spaced and irregular at the poles and thick tectum. Ornamentation microreticulate, lumina less 1 \( \mu m \).

Taxa included: *Scorpiurus muricatus*, *S. vermiculatus*.

5. Discussion of pollen morphology of *Coronilla* and related genera

Pollen Type I is comprised of the genus *Coronilla* and the recently recircumscribed genus *Securigera* (Lassen, 1989a). The type is well defined and easily recognised by its striate-rugulate ornamentation which is very unusual in the pollen of the subfamily Papilionoideae. The pollen of the species placed in *Securigera* differs only from those of *Coronilla* by being slightly larger in size. In view of this, pollen morphology does not help with the delimitation of *Securigera* from *Coronilla*. It is noteworthy that the pollen of *Securigera securidaca* the only species placed in the genus *Securigera* by some workers including Ball (1968) and Chamberlain (1970), but transferred to *Coronilla* by Schmidt (1978), is also indistinguishable from that of *Coronilla* and from the other species recently transferred to *Securigera*.

The genus *Ornithopus* is macromorphologically well defined and it has very distinctive pollen ornamentation and comprises pollen Type II.

Pollen Type III is comprised of the genus *Hippocrepis*. Two more or less distinct subtypes are recognised. No clear macromorphological characters have been found which correlate with these subtypes. The perforate–rugulate subtype could be regarded as a link with the well developed striate–rugulate ornamentation of Type I. It is noteworthy that Lassen (1989a), Lassen (1989b) transferred *Coronilla emerus* and *Coronilla emeroides* to *Hippocrepis* and pollen morphology provides additional evidence to support this re-arrangement.

The geographically isolated *Antopetitia* comprising pollen Type IV although quite distinct in a number of pollen characters shows a very slight similarity in its finely granular–rugulate ornamentation to the distinctive granulate–verrucate ornamentation of *Ornithopus* of pollen Type II. It is noteworthy that Ohashi (1971) links *Antopetitia* palynologically with *Ornithopus* and the pollen data may reflect the close macromorphological relationship reported between the two genera (Polhill, 1981). The macromorphologically specialised *Scorpiurus* comprises pollen Type V and this is the most distinct pollen type in the group. The reticulate ornamentation and the regularly arranged slender, short columellae in the infratectum make this stand out palynologically not only from the rest of the genera in the group but from the pollen of all the genera in tribes Coronilleae and Loteae.

6. A review of the pollen morphology of Loteae and Coronilleae, a key to pollen types and a table summarising the types

In general the apertures and ornamentation of the pollen of *Anthyllis* are very similar to *Lotus* and it is difficult to distinguish all the species in the two genera by pollen morphology. The ornamentation of the four-aperturate species of *Lotus* does differ slightly from *Anthyllis* species with four-aperturate pollen. Similarly *Hymenocarpos* with five–seven aperturate pollen can be distinguished from the palynologically somewhat anomalous North American *Lotus strigosus*. Pseudocolpi are only present in the *Anthyllis vulneraria* group.

*Anthyllis tetraphylla* stands out from the rest of the species with three-aperturate pollen by its comparatively very large pollen. It shows similarities to *Tripodion* (*Hammatolobium*) in having a much thicker exine than occurs in the pollen of the rest of the Loteae/Coronilleae group.

The striate–rugulate exine ornamentation distinguishes the pollen of *Coronilla* and *Securigera* as does the granulate–verrucate ornamentation of *Ornithopus*.

The pollen of a number of the genera that
1a. Pollen with 5–6–(7) apertures ....................................................... 2
b. Pollen with 3–4(–5) apertures .................................................... 3
2a. Ornamentation psilate, finely perforate ................................. *Hymenocarpus circinatus* type (= Anthyllis I)
b. Ornamentation verrucate .............................................................. *Lotus strigosus* type (= Lotus I)
3a. Pollen with 4(–5) apertures ....................................................... 4
b. Pollen with 3(–4) apertures ......................................................... 7
4a. Ornamentation psilate–finely perforate and fossulate .......... *Anthyllis montana* type (= Anthyllis II)
b. Ornamentation striate–rugulate or rugulate–fossulate .......... 5
5a. Ornamentation striate–rugulate .................................................. *Lotus denticulatus* type (= Lotus Iic)
b. Ornamentation rugulate–fossulate ........................................... 6

6a. \(P = 21–29 \mu m\) ............................................................................. *Lotus argophyllus* type (= Lotus Iia)
b. \(P = 18–22 \mu m\) .............................................................................. *Lotus micranthus* type (= Lotus Iib)
7a. \(P = 48–60 \mu m\) ............................................................................. *Anthyllis tetraphylla* type (= Anthyllis III)
b. \(P = 11–42 \mu m\) ............................................................................. 8
8a. Exine 2–3 \(\mu m\) thick, circular in equatorial outline and \(P = 30–41 \mu m\) ................................................................. *Tripodion lotoides* type (= Anthyllis III)
b. Exine 0.5–2 \(\mu m\) thick and elliptical, rectangular, rectangular elliptical and rarely circular in equatorial outline and \(P = 11–34 \mu m\) ................................................................. 9
9a. Rectangular in equatorial outline ........................................ 10
b. Elliptical or rectangular–elliptical (sometimes circular) in equatorial outline ............................................................ 12
10a. Ornamentation granulate–verrucate ................................. *Ornithopus perpusillus* type (= Coronilla II)
b. Ornamentation psilate, perforate and/or fossulate .............. 11
11a. \(P = 21–26 \mu m\) ............................................................................. *Anthyllis gerardii* type (= Anthyllis Iva; *Dorycniopsis*)
b. \(P = 27–36 \mu m\) ............................................................................. *Cytisopsis dorycnifolia* type (= Anthyllis Ivb)
12a. Ornamentation striate–rugulate ........................................... 13
b. Ornamentation reticulate, perforate–rugulate or psilate–perforate and/or fossulate ......................................................... 14
13a. Ornamentation striate–rugulate over all the pollen and endoaperture clearly lalongate, (2–6) \((5–14) \mu m\) ........................................ *Coronilla varia* type (= Coronilla I)
b. Ornamentation striate–rugulate at the mesocolpium and psilate perforate at the poles and endoaperture almost circular, (7–8) \((9–10) \mu m\) ........................................ *Vermifrux abyssinica* type (= Lotus Iic)
14a. Ornamentation finely reticulate ................................................ *Scorpiurus muricatus* type (= Coronilla V)
b. Ornamentation perforate, perforate–rugulate, perforate–finely granulate rugulate, psilate–perforate and/or fossulate ......................................................... 15
15a. With pseudocolpi ................................................................. *Anthyllis vulneraria* type (= Anthyllis Ivc)
b. Without pseudocolpi ................................................................................................................................. 16
16a. \(P = 32–38(X > 34) \mu m\) ............................................................... *Pseudolotus makranicus* type (= Lotus Iia)
b. \(P = 11–35(X < 30) \mu m\) ............................................................... 17
17a. With granules at colpus margin ........................................... *Lotus crassifolius* type (= Lotus IId; *Hosackia*)
b. Without granules at colpus margin ..................................... 18
18a. Endoapertures of (1–5) \((3–10) \mu m\) ......................................... *Lotus creticus* type (= Lotus Iib and *Hippocrepis* type (= Coronilla IId and Coronilla Iib)
b. Endoapertures of (5–10) \((5–15) \mu m\) ......................................... *Podolotus hosackioides* type (= Lotus Iic), *Anthyllis cytooides* type (= Anthyllis Ivd) and *Antopetitia* (Coronilla IV)

The types are summarised in Table 2.
have been segregated from *Anthyllis* including *Dorycnopsis* and *Cytisopsis* can be distinguished by shape and size.

*Vermifrux* has pollen with distinct striate–rugulate ornamentation at the equator and psilate–perforate ornamentation at the poles.

*Scorpiurus* has very distinctive pollen with reticulate ornamentation. While *Pseudolotus* is distinguished by its comparatively large three-aperturate pollen.

The differences in the pollen morphology between the North American species of *Lotus* (subgenus Hosackia) with three apertures and the majority of the Old World species of *Lotus* and also *Acmispon roudairei*, the *Anthyllis cytisoides* group, *Hippocrepis*, *Podolotus* and the tropical African *Antopetita* are very small as can be seen summarised in the general key to pollen types of the whole Loteae/Coronilleae group that follows.

The pollen types described for the *Anthyllis* group (Diez and Ferguson, 1991), the *Lotus* group (Diez and Ferguson, 1994) and the *Coronilla* group are combined together into a single key.

7. General discussion and systematic conclusions

The pollen morphology of the majority of the genera placed in the tribes Loteae and Coronilleae of Polhill (1981) is relatively distinctive, particularly the exine stratification where there is a well development endexine, foot layer very reduced or absent, short, irregularly spaced columellae or large granules in the infratectum and a complete and thick tectum. This type of stratification is regarded as rather specialised by Ferguson and Skvarla (1981), Ferguson and Skvarla (1983) and Guinet and Ferguson (1989). The frequently occurring psilate ornamentation especially but also the striate–rugulate and fossulate–rugulate or even granulate–verrucate ornamentation found in *Ornithopus* are also distinctive and this combination of exine stratification and ornamentation type does not occur in other groups of the subfamily Papilionoideae. Psilate ornamentation does occur in the tribe Phaseoleae especially in the subtribe Diocleiinae where it is regarded as a “derived” character (Kavanagh and Ferguson, 1981).

Within the Loteae/Coronilleae aperture number and exine ornamentation are the most useful pollen characters for dividing the group (see the key to pollen types). In *Anthyllis* and related genera there is a trend towards increase in aperture number from three-colporate to three-colporate with pseudocolpi to four-colporate and to six–seven colporate. A similar trend occurs in *Lotus* and closely related genera. Three-colporate pollen is widespread but most of the western North American species have four-colporate, or less commonly six-colporate pollen. Only those North America taxa that have been put into subgenus Hosackia have three-colporate pollen. This parallel in increasing aperture number between the primarily Mediterranean *Anthyllis* group and the North American *Lotus* group is noteworthy. Guinet and Ferguson (1989) have suggested than an increase in aperture number in the pollen of Leguminosae is indicative of specialisation and it would appear that the trend has evolved independently in the geographically and taxonomically separate lines in the tribe Loteae of Polhill (1981).

It is perhaps remarkable that there is no variation in aperture number in the *Coronilla* group (tribe Coronilleae of Polhill, 1981). However, there is far more variation in the exine ornamentation in this group than in the Loteae. The striate–rugulate ornamentation in *Coronilla* and *Securigera* is very rare in the subfamily Papilionoideae. Apart from occurring in a few North American species of *Lotus* and in *Vermifrux* it is only found in the taxonomically very remote tribe Swartzieae (Ferguson and Skvarla, 1991).

The striate–rugulate exine ornamentation in the three closely related North American species of *Lotus*, *L. denticulatus*, *L. humistratus* and *L. wrangelianus* is somewhat paralleled in the African genus *Vermifrux*. The pollen of the North American species of *Lotus* subgenus Hosackia is three-colporate which is distinguishable from the pollen of the Old World species of *Lotus* only by the presence of granules at the colpus margins. It is noteworthy that Crompton and Grant (1993) believe that the pollen of the Hosackia group is more closely related to that of the North American species than to the Old World taxa. However, these problems highlight the need for a complete taxonomic review
Table 2
Summary of the major pollen characters used to distinguish all the types and subtypes recognised in the Loteae and Coronilleae (see Diez and Ferguson, 1991, Diez and Ferguson, 1994) and listing the taxa included. The arrangement of the types follows the order of the key to pollen types. Similar pollen types are placed adjacent to each other using aperture number and exine ornamentation as the primary distinguishing characters. Measurements are in μm and only the ranges for the polar (P) and (E) are given and P/E indicates the shape index.

<table>
<thead>
<tr>
<th>Type</th>
<th>Description</th>
<th>Aperture Details</th>
<th>Taxa Included</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anthyllis I</td>
<td>(Hymenocarpos circinatus type)</td>
<td>Apertures 6 (~7), ornamentation psilate, finely perforate.</td>
<td>Anthyllis cornicina, A. lotoides, Hymenocarpos circinatus</td>
</tr>
<tr>
<td>Lotus I</td>
<td>(Lotus strigosus type)</td>
<td>Apertures 5 (~6), ornamentation verrucate.</td>
<td>Lotus strigosus</td>
</tr>
<tr>
<td>Anthyllis II</td>
<td>(Anthyllis montana type)</td>
<td>Apertures 4 (~5), ornamentation psilate, finely perforate and fossulate.</td>
<td>Anthyllis barba-jovis, A. hamosa, A. henoniana, A. hermanniae, A. montana, subsp. hispanica, subsp. jacquinii, subsp. montana</td>
</tr>
<tr>
<td>Anthyllis IVC</td>
<td>(Anthyllis vulneraria type)</td>
<td>Apertures 3, ornamentation striate rugulate.</td>
<td>Anthyllis gerardii</td>
</tr>
<tr>
<td>Coronilla V</td>
<td>(Scorpiurus muricatus type)</td>
<td>Apertures 3, ornamentation finely reticulate.</td>
<td>Scorpiurus muricatus, S. vermiculatus</td>
</tr>
</tbody>
</table>

**Anthyllis I (Hymenocarpos circinatus type)**

Apertures 6 (~7), ornamentation psilate, finely perforate. \( P \times E = (21–32) \times (18–34); \ P/E = 0.82–1.36, \) suboblate to subprolate rarely prolate

Taxa included: Anthyllis cornicina, A. lotoides, Hymenocarpos circinatus

**Lotus I (Lotus strigosus type)**

Apertures 5 (~6), ornamentation verrucate. \( P \times E = (22–33) \times (24–38); \ P/E = 0.81–1.00, \) suboblate to spheroidal

Taxa included: Lotus strigosus

**Anthyllis II (Anthyllis montana type)**

Apertures 4 (~5), ornamentation psilate, finely perforate and fossulate. \( P \times E = (20–33) \times (20–34); \ P/E = 0.75–1.28, \) suboblate to subprolate

Taxa included: Anthyllis barba-jovis, A. hamosa, A. henoniana, A. hermanniae, A. montana, subsp. hispanica, subsp. jacquinii, subsp. montana

**Lotus IIa (Lotus argophyllus type)**

Apertures 4, ornamentation rugulate fossulate. \( P \times E = (20–33) \times (19–30); \ P/E = 0.86–1.20, \) suboblate to subprolate

Taxa included: Lotus argophyllus, L. benthamii, L. grandiflorus, L. hermannii, L. junceus, L. nevadensis, L. rigidus, L. salisuginosus, L. scoparius, L. strigosus var. tomentellus, L. wrightii

**Lotus Ib (Lotus micranthus type)**

Apertures 4, ornamentation psilate perforate. \( P \times E = (18–22) \times (17–23); \ P/E = 0.86–1.11, \) suboblate to spheroidal

Taxa included: Lotus haydonii, L. micranthus, L. purshianus

**Anthyllis III (Anthyllis tetraphylla type)**

Apertures 3 (~4), ornamentation psilate perforate. \( P \times E = (30–60) \times (30–60); \ P/E = 0.79–1.18, \) suboblate to spheroidal. Exine 2–3 μm thick

Taxa included: Triphopion (Anthyllis) tetraphylla, T. (Hammatolobium) kremerianum, T. (Hammatolobium) graecum

**Coronilla II (Ornithopus perpusillus type)**

Apertures 3, ornamentation granulate, verrucate and perforate. \( P \times E = (18–30) \times (17–25); \ P/E = 1.0–1.58, \) spheroidal to prolate. Exine 1–2 μm thick

Taxa included: O. compressus, O. isthmocarpus, O. perpusillus, O. pinnatus, O. satiusus, O. uncinatus

**Anthyllis Iva (Anthyllis gerardii type)**

Apertures 3, ornamentation psilate, perforate and fossulate. \( P \times E = (21–26) \times (21–26); \ P/E = 0.95–1.18, \) spheroidal

Taxa included: Anthyllis gerardii

**Anthyllis IVb (Cytisopsis dorycnifolia type)**

Apertures 3, ornamentation psilate fossulate. \( P \times E = (27–36) \times (23–34); \ P/E = 1.00–1.20, \) spheroidal to subprolate

Taxa included: Cytisopsis ahmedii, C. dorycnifolia

**Coronilla I (Coronilla varia type)**

Apertures 3, ornamentation striate rugulate. \( P \times E = (14–29) \times (9–25); \ P/E = 1.0–1.8, \) spheroidal to strongly prolate. Endoapertures lalongate (2–6) \times (5–14) μm


**Lotus IIIe (Vermifrux abyssinica type)**

Apertures 3, ornamentation striate rugulate on mesocolpium, psilate on poles. \( P \times E = (20–27) \times (20–25); \ P/E = 0.9–1.13, \) spheroidal

Endoapertures circular (7–8) \times (9–10) μm

Taxa included: Vermifrux abyssinica

**Coronilla V (Scorpiurus maticatus type)**

Apertures 3, ornamentation finely reticulate. \( P \times E = (18–24) \times (12–16); \ P/E = 1.12–1.76, \) spheroidal to strongly prolate

Taxa included: Scorpiurus maticatus, S. vermiculatus

**Anthyllis Ivc (Anthyllis vulneraria type)**
Table 2 (continued)

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation psilate, finely perforate. $P \times E = (24-42) \times (23-38)$; $P/E = 0.96-1.33$, spheroidal to subprolate or prolate. Pseudocolpi present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa included: Anthyllis cherleri, A. polycephala, A. ramburii, A. tejeodensi, A. vulneraria, subsp. maura, subsp. vulneraria</td>
</tr>
</tbody>
</table>

**Lotus IIIa (Pseudolotus makranicus type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation psilate perforate. $P \times E = (32-38) \times (30-37)$; $P/E = 0.94-1.12$, spheroidal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa included: Pseudolotus makranicus</td>
</tr>
</tbody>
</table>

**Lotus IIIb (Lotus crassifolius type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation psilate perforate with granules around the colpus margin. $P \times E = (18-23) \times (16-20)$; $P/E = 1.00-1.35$, spheroidal prolate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa included: Lotus crassifolius, L. oblongifolius, L. stipularis</td>
</tr>
</tbody>
</table>

**Coronilla IIIa and Coronilla IIIb (Hippocrepis type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation perforate or perforate rugulate. $P \times E = (15-28) \times (12-26)$; $P/E = 0.87-1.66$, spheroidal to strongly prolate</th>
</tr>
</thead>
</table>

**Lotus IIIb (Lotus creticus type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation psilate perforate. $P \times E = (11-31) \times (7-31)$; $P/E = 0.95-1.90$, spheroidal to strongly prolate</th>
</tr>
</thead>
</table>

**Lotus IIIc (Podolotus hosackioides type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation psilate perforate and fossulate. $P \times E = (23-34) \times (24-29)$; $P/E = 0.88-1.21$, suboblate to subprolate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa included: Acmispon roudairei, Podolotus hosackioides</td>
</tr>
</tbody>
</table>

**Anthyllis IVd (Anthyllis cytisoides type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation psilate perforate or finely fossulate. $P \times E = (24-35) \times (20-32)$; $P/E = 0.93-1.50$, spheroidal to prolate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa included: Anthyllis aurea, A. cytisoides, A. terniflora</td>
</tr>
</tbody>
</table>

**Coronilla IV (Antopetitia type)**

<table>
<thead>
<tr>
<th>Apertures 3, ornamentation perforate, finely granular–rugulate at mesocolpium and more or less psilate at apocolpium. $P \times E = (20-26) \times (21-26)$; $P/E = 0.86-1.09$, suboblate–spheroidal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxa included: Antopetitia abyssinica</td>
</tr>
</tbody>
</table>

of relationships in *Lotus* and its closely related genera.

Although there have been many studies of the group, workers since Bentham (1865) have tended to focus their attention primarily on regional studies often at species level and below and there is a need to evaluate the similarities and differences that occur in a wide range of characters in both the Old World and the New World taxa before generic boundaries can be firmly established. This has been pointed out to same extent by Isely (1981) and more recently Lassen (1989a; pers. commun.) who is currently revising much of the group.

Hippocrepis with two types of pollen ornamentation is somewhat intermediate; one group of the species with rugulate–fossulate ornamentation slightly resembles Coronilla while the other group with a perforate tectum is more similar to Lotus.

The pollen morphology of Scorpiurus is rather anomalous in the tribes both in ornamentation and stratification. The pollen is of a more generalised type and it could point to need to re-evaluate the position of the genus in the Loteae/Coronilleae. Ferguson and Skvarla (1981) have suggested that there is some evidence from pollen morphology for keeping separate the tribes Coronilleae and Loteae. They based this view on results from the pollen of Hymenocarpos, Lotus and only Scorpiurus from the Coronilla group. The latter genus has been shown to have atypical pollen. Overall there
appears to be little evidence from comparative pollen morphological studies to support upholding two distinct tribes. The data from the present investigation, especially from the exine stratification, suggest a broad interpretation of the tribe Loteae as adopted by Lassen (1989a) and followed by Lock (1989) and Lock and Simpson (1991) would be more appropriate.

The Coronilleae/Loteae are placed near to other temperate tribes including Cicereae, Trifolieae and Vicieae (Polhill, 1981). The pollen of these tribes shows similarities to Loteae/Coronilleae in size, shape, thin exine, exine thinner at the poles in comparison with the equator and also differences between the ornamentation on the poles and the equator (Clarke and Kupicha, 1976). The exine stratification of the Vicieae, particularly the well developed endexine, sometimes granular infratectum and often complete tectum (Ferguson, 1985) does resemble Loteae but the foot layer is rarely completely absent and as also occurs in Trifolieae where the tectum is usually reticulate or reticulate–rugulate. Some species of Trifolium do have a more or less psilate–perforate tectum (Muñoz Rodriguez, 1990) but the exine stratification appears to differ having regular, distinct columellae (Ferguson and Skvarla, 1981). Cicer has pollen with reticulate ornamentation and exine stratification with distinct regular columellae (Ferguson and Skvarla, 1981).

Doyle et al. (1995) have shown from molecular systematic studies that the Loteae/Coronilleae group show unexpected results in having similarities with predominantly tropical tribes including Phaseoleae and Millettieae and not with those tribes with temperate distribution and herbaceous habit with which they have long been considered to be related. It has been pointed out in the present palynological investigation that many of the pollen characters in Loteae/Coronilleae are “derived” and in many ways the data from pollen morphology are not inconsistent with the molecular systematic findings. The similarities in pollen between some tropical tribes, particularly Phaseoleae, and the Loteae/Coronilleae could be considered as indicative of as much phylogenetic relationship between these groups as there is with the temperate tribes with which Loteae/Coronilleae have been traditionally placed.

However, as Doyle et al. (1992) point out only when more characters are investigated and homologies more fully analysed can the phylogenetic relationships between Loteae/Coronilleae and temperate and tropical group be understood.

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References


