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Tadauchi, Osamu

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FACTOR ANALYSIS OF INTEGUMENTAL SCULPTURES IN THE JAPANESE ANDRENID BEES*

OSAMU TADAUCHI

Entomological Laboratory, Faculty of Agriculture,
Kyushu University, Fukuoka 812, Japan

Abstract

Character correlations in 50 characters of integumental sculptures derived from 85 taxa or OTU's of the genus *Andrena* (Hymenoptera, Andrenidae) of Japan were analyzed by factor analysis with varimax rotation. Nine common factors were extracted explaining 73.08 percent of the total variance among the characters. Nine character associations affected by the common factors seemed structurally related. The associations were assumed to be the following indices: the sparseness of punctures on the thorax, the development of the pronotal suture or angle, the development of tessellation on the metasoma, the roughness of the integument, the development of punctation on the clypeus, the appearance of wrinkles on the lateral portion of the thorax, the appearance of spines on the hind femur, the distinctness of the facial fovea, and the development of punctation on the metasomal terga.

Introduction

It was shown in a previous paper (Tadauchi, 1982) that the study of character correlations by factor analysis is valuable in evolutionary studies. When characters investigated are based on regional or limited sources, the character associations extracted by factor analysis seem to be biologically meaningful and provide insight into the limiting factors affecting the original characters.

The present study was designed to observe the integumental sculptures in the Japanese Andrenid bees with the same method used in the above mentioned paper. The surface sculptures such as punctation, tessellation, carination, reflection, and rugosity are one of the most useful character groups used for the taxonomy in the genus *Andrena*. The purpose of this study is to group characters based on the magnitude of correlations and to find the biological meaning of common factors extracted by factor analysis.

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Material and Method

Eighty-five taxa or OTU's of the genus *Andrena* (Hymenoptera, Andrenidae) of Japan were used. The names and the code numbers of OTU's are shown in Table 4. Fifty female characters of sculptures listed in Table 1 were coded and then processed on FACOM M-ZOO computer in the Computer Center of Kyushu University.

Factor analysis was performed based on the correlation matrix of the 50 characters of integumental sculptures. In the present study the varimax orthogonal method (Kaiser, 1958) was used. Adequate discussions of the computational procedures and associated techniques may be found in Thurstone (1947), Seal (1964), and Asano (1971).

Results and Discussion

A correlation matrix among the 50 sculptures was calculated to a component analysis. The eigenvalue, the percentage of the total variance among the characters contributed by each component, and the accumulated percentage are shown in Table 2. Nine eigenvalues accounting for 73.08 percent of the total variance in a correlation matrix were obtained. The factor loading matrix rotated by the varimax solution is given in Table 3. These rotated factors contain the same information as the unrotated factors but represent it in a more convenient manner. The factor loading coefficients are the correlations of characters with the component axes. It is possible to assemble the characters, as shown in the study of 40 characters of hairs (Tadauchi, 1982), which have highest positive or negative loadings for corresponding common factors. The nine character groups are listed in the decreasing order of their loadings for corresponding factors. The results are summarized in Figs. 1-9, where the character codes associated with the highest loadings of more than 0.50 for each factor are given. A minus sign indicates a negative loading and a plus one indicates a positive loading. A character code in parentheses represents higher correlation with another factor. A character code within square brackets indicates a character with a correlation of less than 0.50 for the factor, which, however, has still lower correlations with the other factors. Characters which exhibited a highest correlation of less than 0.50 are only loosely associated with any of the nine factor groups and may be considered as having essentially independent variation. In the following result and discussion two numbers in parentheses after a character name indicate the code number of the character and the factor loading score for the character.

First character group (Fig. 1) holding highest negative loadings for Factor I contains only two characters. They are the puncture density on the *medial meso-*

Table 1. Fifty characters of integumental sculptures used in the present study with the code numbers and the numbers of the states for the characters.

| | | |
|-----|--|---|
| 1. | Existence of median longitudinal impunctate line on clypeus | 3 |
| 2. | Size of punctures on clypeal median area | 3 |
| 3. | Strength of punctures on clypeal median area | 4 |
| 4. | Density of punctures on clypeal median area | 3 |
| 5. | Degree of separation of facial fovea from eye margin | 3 |
| 6. | Depth of facial foveae | 2 |
| 7. | Strength of frontal line | 3 |
| 8. | Strength of lugulae on upper paraocular areas | 3 |
| 9. | Density of punctures on vertex | 3 |
| 10. | Strength of punctures on genal area | 3 |
| 11. | Tessellation on genal area | 5 |
| 12. | Curvature of hypostomal carina | 4 |
| 13. | Strength of hypostomal carina | 4 |
| 14. | Strength of humeral angle on pronotum | 3 |
| 15. | Length of pronotal suture | 3 |
| 16. | Strength of pronotal suture | 3 |
| 17. | Existence of emargination on antero-medial portion on pronotum | 3 |
| 18. | Existence of lateral lugulae on pronotum | 2 |
| 19. | Size of punctures on medial mesoscutum | 3 |
| 20. | Strength of punctures on medial mesoscutum | 3 |
| 21. | Density of punctures on medial mesoscutum | 3 |
| 22. | Tessellation on medial mesoscutum | 3 |
| 23. | Density of punctures on scutellum | 3 |
| 24. | Tessellation on scutellum | 4 |
| 25. | Strength of punctures on mesepisternum | 3 |
| 26. | Tessellation on medial-posterior mesepisternum | 5 |
| 27. | Size of propodeal enclosure | 3 |
| 28. | Distinctness of boundary of propodeal enclosure | 3 |
| 29. | Rugosity on propodeal enclosure | 5 |
| 30. | Existence of a carina on posterior area of propodeal enclosure | 2 |
| 31. | Angle of posterior propodeum seen laterally | 3 |
| 32. | Tessellation on dorsal face of propodeum | 5 |
| 33. | Existence of lateral keels on dorso-lateral face of propodeum | 2 |
| 34. | Rugosity on corbicula area | 4 |
| 35. | Tessellation on posterior tegulae | 4 |
| 36. | Existence of spines near apex of hind femur | 2 |
| 37. | Curvature of posterior spurs on hind tibiae | 3 |
| 38. | Strength of punctures on 1st metasomal tergum | 5 |
| 39. | Density of punctures on 1st metasomal tergum | 4 |
| 40. | Tessellation on 1st metasomal tergum | 4 |
| 41. | Strength of punctures on 3rd metasomal tergum | 4 |
| 42. | Density of punctures on basal portion of 3rd metasomal tergum | 4 |
| 43. | Tessellation on 3rd metasomal tergum | 4 |
| 44. | Strength of posterior depression on 3rd metasomal tergum | 3 |
| 45. | Width of posterior depression of 3rd metasomal tergum | 4 |
| 46. | Existence of reflection on apex of 3rd metasomal tergum | 2 |
| 47. | Distinctness of triangular area of pygidial plate | 4 |
| 48. | Strength of punctures on 3rd metasomal sternum | 3 |
| 49. | Tessellation on 3rd metasomal sternum | 3 |
| 50. | Number of graduli on metasomal sterna | 5 |

Table 2. Eigenvalues, percentages and accumulated percentages of the total variance among the 50 integumental sculptures contributed by each component with eigenvalue greater than 1.0.

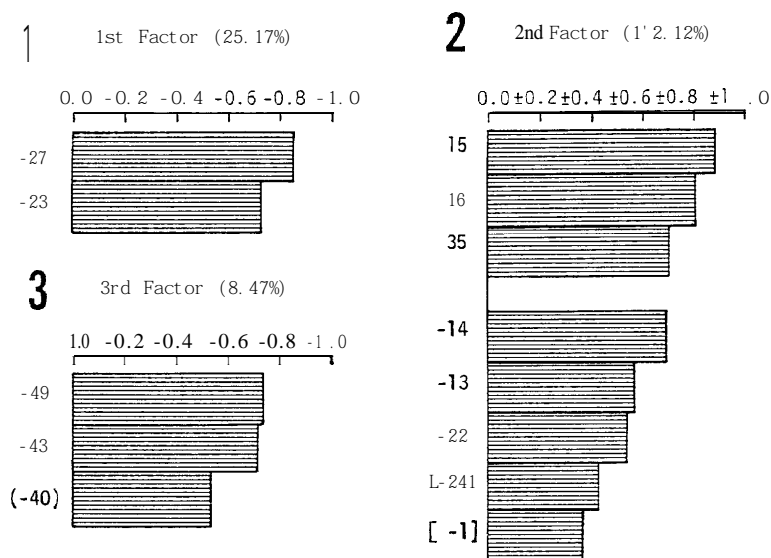
| Component | Eigenvalue | Percentage | Accumulated percentage |
|-----------|------------|------------|------------------------|
| 1 | 12.59 | 25.17 | 25.17 |
| 2 | 6.01 | 12.02 | 37.19 |
| 3 | 4.23 | 8.47 | 45.66 |
| 4 | 3.03 | 6.05 | 51.71 |
| 5 | 2.88 | 5.76 | 57.47 |
| 6 | 2.73 | 5.45 | 62.93 |
| | 1.94 | 3.88 | 66.80 |
| 8 | 1.72 | 3.45 | 70.25 |
| | 1.41 | 2.83 | 73.08 |
| 10 | 1.31 | 2.62 | 75.70 |
| 11 | 1.09 | 2.19 | 77.89 |

scutum (21, -0.86) and the *puncture density on the scutellum* (23, -0.73). Among six characters as for the density of punctures used in the present study, two from the thorax are strongly connected with this factor. The correlation value of 0.58 is obtained between these two characters. The closer examination of the original matrix shows that the densities of punctures derived from different regions have considerably low correlations with one another. For instance, the puncture density of the mesoscutum has the value of 0.15 with that of the clypeus (4), -0.06 with that of the vertex (9), 0.33 with that of the first metasomal tergum (39), and 0.12 with that of the third metasomal tergum (42). However, between the puncture densities of the first and third metasomal terga the correlation value is found to be 0.70. Therefore it shows that the puncture densities on the different regions of the body have their own independent variations with one another. This factor seems to be connected with the puncture density on the thorax. The matrix also reveals that the puncture density on the thorax has moderate correlations ranging from 0.24 to 0.45 with the size (19) and the strength (20) of punctures on the thorax. The puncture density does not have correlations with the tessellation on the thorax (22 and 24), as it shows from -0.10 to 0.16. When this association affected by the Factor I is highly developed, it will probably lead to a much-punctured thorax of the body.

Second character association (Fig. 2) holding highest positive and negative loadings for Factor II includes the *length of the pronotal suture* (15, 0.90), the *strength of the pronotal suture* (16, 0.82), the *tessellation of the posterior tegulae* (35, 0.72), the *strength of the humeral angle of the pronotum* (14, -0.71), the *strength of the hypostomal carina* (13, -0.58), and the *tessellation of the medial mesoscutum* (22, -0.55). Since this group is composed of various characters, it is difficult to interpret this factor biologically as a whole. However the noticeable result is

Table 3. Factor loading matrix rotated by varimax solution based on 50 characters of integumental sculptures derived from 85 OTU's of the Japanese andrenid bees.

| Character code number | Rotated factors | | | | | | | | |
|-----------------------|-----------------|--------|--------|--------|--------|--------|--------|--------|--------|
| | I | II | III | IV | V | VI | VII | VIII | IX |
| 1 | -0.111 | -0.366 | -0.156 | 0.023 | 0.131 | 0.035 | -0.131 | 0.355 | -0.029 |
| 2 | -0.078 | 0.082 | 0.097 | -0.127 | 0.868 | 0.072 | -0.286 | 0.076 | 0.048 |
| 3 | 0.042 | -0.089 | 0.120 | -0.155 | 0.862 | -0.030 | -0.104 | -0.034 | 0.210 |
| 4 | -0.026 | 0.018 | -0.043 | -0.128 | 0.812 | -0.125 | 0.046 | 0.065 | 0.200 |
| 5 | 0.074 | 0.223 | 0.087 | -0.171 | -0.112 | 0.045 | -0.103 | -0.846 | 0.095 |
| 6 | -0.263 | 0.156 | 0.244 | -0.176 | -0.162 | -0.310 | -0.121 | -0.666 | -0.183 |
| 7 | 0.046 | -0.154 | -0.037 | -0.086 | 0.693 | -0.194 | 0.057 | -0.065 | 0.287 |
| 8 | -0.074 | -0.079 | 0.085 | 0.338 | 0.252 | 0.525 | 0.294 | 0.028 | 0.059 |
| 9 | 0.170 | -0.049 | 0.068 | -0.279 | 0.175 | -0.388 | 0.104 | -0.575 | 0.340 |
| 10 | -0.033 | -0.223 | 0.112 | -0.541 | 0.159 | -0.539 | -0.068 | -0.342 | 0.140 |
| 11 | 0.012 | 0.455 | -0.114 | 0.490 | 0.026 | 0.005 | -0.133 | 0.144 | -0.306 |
| 12 | -0.139 | -0.028 | 0.109 | 0.142 | -0.126 | 0.031 | -0.095 | 0.001 | -0.010 |
| 13 | -0.137 | -0.583 | 0.379 | 0.295 | 0.235 | 0.003 | -0.019 | 0.132 | 0.048 |
| 14 | 0.173 | -0.710 | 0.060 | -0.061 | 0.314 | -0.060 | -0.162 | 0.162 | -0.152 |
| 15 | -0.078 | 0.896 | 0.024 | -0.078 | -0.071 | 0.116 | -0.045 | -0.041 | 0.028 |
| 16 | -0.116 | 0.819 | 0.091 | -0.096 | 0.035 | 0.146 | 0.170 | -0.120 | -0.016 |
| 17 | 0.061 | 0.162 | 0.107 | -0.126 | 0.288 | -0.125 | 0.077 | -0.036 | 0.095 |
| 18 | 0.056 | -0.158 | 0.105 | 0.066 | 0.103 | -0.936 | 0.005 | -0.077 | 0.087 |
| 19 | -0.219 | 0.037 | -0.020 | -0.497 | 0.504 | -0.117 | 0.080 | -0.089 | 0.359 |
| 20 | -0.319 | 0.344 | -0.042 | -0.475 | -0.033 | -0.390 | 0.064 | -0.092 | 0.376 |
| 21 | -0.858 | -0.001 | -0.053 | -0.174 | 0.135 | 0.057 | -0.032 | 0.009 | 0.089 |
| 22 | -0.285 | -0.548 | -0.212 | 0.333 | 0.107 | 0.071 | -0.138 | -0.010 | -0.448 |
| 23 | -0.731 | 0.359 | 0.010 | -0.079 | -0.056 | 0.032 | -0.093 | 0.006 | 0.233 |
| 24 | -0.250 | -0.436 | 0.097 | 0.358 | -0.053 | -0.102 | -0.213 | 0.209 | -0.440 |
| 25 | -0.055 | 0.118 | 0.206 | -0.571 | 0.217 | -0.469 | 0.085 | -0.062 | 0.412 |
| 26 | -0.381 | -0.172 | -0.137 | 0.471 | 0.069 | 0.301 | -0.293 | 0.282 | -0.235 |
| 27 | 0.094 | 0.270 | -0.096 | -0.157 | -0.710 | 0.034 | -0.234 | -0.130 | 0.025 |
| 28 | -0.172 | 0.120 | -0.011 | -0.367 | 0.325 | -0.374 | -0.164 | 0.195 | 0.367 |
| 29 | -0.113 | 0.257 | -0.081 | -0.554 | -0.383 | -0.280 | -0.226 | -0.340 | 0.277 |
| 30 | -0.098 | -0.047 | 0.134 | -0.907 | 0.232 | 0.031 | -0.018 | -0.122 | 0.037 |
| 31 | 0.082 | 0.386 | 0.160 | -0.734 | -0.133 | 0.059 | -0.118 | 0.001 | 0.083 |
| 32 | -0.325 | 0.128 | -0.257 | -0.236 | 0.202 | -0.035 | -0.616 | 0.050 | 0.071 |
| 33 | 0.056 | -0.158 | 0.105 | 0.066 | 0.103 | -0.936 | 0.005 | -0.077 | 0.087 |
| 34 | -0.064 | 0.113 | 0.115 | -0.720 | 0.186 | -0.153 | 0.165 | -0.253 | 0.272 |
| 35 | -0.142 | 0.721 | -0.088 | 0.007 | 0.157 | -0.018 | -0.228 | 0.010 | -0.047 |
| 36 | 0.026 | 0.101 | 0.001 | -0.032 | -0.055 | 0.050 | 0.880 | 0.098 | 0.059 |
| 37 | -0.022 | 0.046 | -0.006 | -0.430 | 0.179 | -0.495 | 0.491 | 0.117 | 0.147 |
| 38 | -0.279 | 0.197 | 0.169 | -0.213 | 0.387 | -0.178 | -0.044 | 0.129 | 0.669 |
| 39 | -0.246 | 0.087 | -0.078 | -0.062 | 0.344 | -0.003 | -0.116 | 0.128 | 0.763 |
| 40 | -0.027 | -0.171 | -0.525 | 0.134 | -0.072 | 0.129 | -0.148 | 0.203 | -0.618 |
| 41 | -0.096 | -0.018 | 0.187 | -0.394 | 0.298 | -0.127 | 0.072 | -0.186 | 0.699 |
| 42 | -0.037 | -0.133 | 0.072 | -0.054 | 0.119 | -0.039 | 0.033 | -0.072 | 0.866 |
| 43 | -0.078 | -0.044 | -0.716 | 0.247 | -0.006 | 0.164 | -0.059 | 0.143 | -0.445 |
| 44 | -0.151 | 0.063 | 0.093 | -0.828 | 0.154 | 0.074 | -0.038 | -0.053 | 0.051 |
| 45 | -0.341 | -0.030 | 0.136 | -0.279 | -0.155 | 0.347 | 0.034 | -0.151 | 0.282 |
| 46 | -0.064 | -0.017 | 0.111 | -0.632 | 0.110 | 0.046 | -0.093 | -0.036 | 0.103 |
| 47 | 0.094 | -0.073 | -0.012 | 0.133 | -0.109 | 0.214 | -0.107 | 0.011 | -0.231 |
| 48 | -0.170 | 0.091 | 0.244 | -0.237 | 0.323 | -0.265 | -0.141 | -0.148 | 0.230 |
| 49 | -0.026 | 0.118 | -0.744 | 0.289 | -0.147 | 0.094 | -0.038 | 0.122 | -0.005 |
| 50 | -0.026 | 0.170 | -0.274 | -0.063 | 0.427 | -0.131 | -0.138 | -0.034 | 0.005 |



Figs. 1-3. Factor loadings of higher loading sculpture characters for the first to the third common factors extracted by factor analysis with varimax rotation. The numbers on the left side indicate the code numbers for the characters.

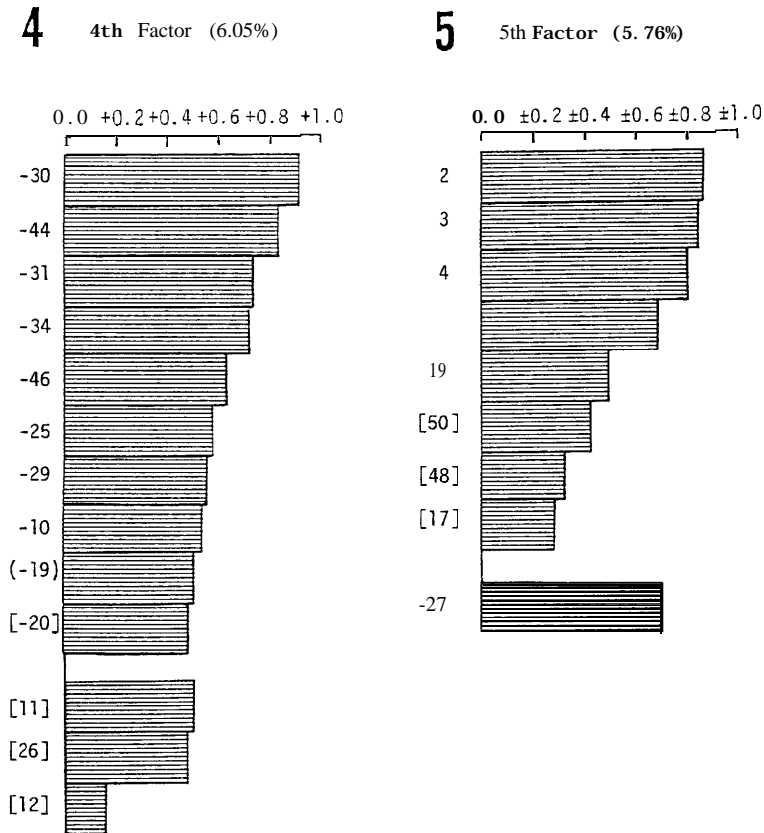
that the three characters on the pronotum (14, 15, and 16) have considerably high scores for this factor. The two characters of the pronotal suture have high negative correlations with the strength of the humeral angle having the value of -0.60 and -0.61. Therefore the positive direction of the factor will lead to a construction of a longer and stronger pronotal suture and a weaker humeral angle.

Third character group (Fig. 3) affected by Factor III is made up of the following characters : *the tessellation of the third metasomal sternum* (49, -0.74), *the tessellation of the third metasomal tergum* (43, -0.72) and *the tessellation of the first metasomal tergum* (40, -0.53). Among six characters concerning the tessellation on the thorax and metasoma (22, 24, 26, 40, 43, and 49), three characters restricted to the metasoma are extracted by this analysis. The values of the factor loading for the tessellations of the mesoscutum (22), scutellum (24), and mesepisternum (26) are observed to be -0.21, 0.10 and -0.14, respectively. Concerning the characters of tessellation the five ones except for the tessellation of the third metasomal sternum, which has the highest connection with the third factor, have moderate to high correlations (0.28-0.73) with one another. As for the tessellation of the third metasomal sternum, it has moderate correlations with those of the first and third metasomal terga having the value of 0.36 and 0.57. However it has very low correlations with the three tessellated characters on the thorax showing the value of 0.06, 0.20 and 0.25. The tessellated characters on the metasoma have their independent varia-

tions against those on the thorax. Therefore this factor seems to be related to the tessellation of the metasoma. When the character association is developed, the metasomal terga and sterna will become densely tessellate.

Fourth character group (Fig. 4) holding highest negative loadings for Factor IV consists of *the existence of a carina on the posterior area of the propodeal enclosure* (30, -0.91), *the strength of posterior depression on the third metasomal tergum* (44, -0.83), *the angle of the posterior propodeum seen from side* (31, -0.73), *the rugosity on the corbicula area* (34, -0.72), *the existence of reflection on the apex of the third metasomal tergum* (46, -0.63), *the strength of punctures on the mesepisternum* (25, -0.57), *the rugosity of the propodeal enclosure* (29, -0.55), *the strength of punctures on the genal area* (10, -0.54), *the size of punctures on the medial mesoscutum* (19, -0.50) and *the strength of punctures on the medial mesoscutum* (20, -0.48). The moderate positive loadings for this factor are obtained from *the tessellation on the genal area* (11, 0.49), and *the tessellation on the medial-posterior portion of the mesepisternum* (26, 0.47). This character assemblage is related to the roughness of the integument. At the higher score level the factor is particularly concerned with the carination, depression, rugosity and reflection of the integument. Among seven characters concerning the strength of punctures (3, 10, 20, 25, 38, 41, 48), three from the genal area (10), the mesoscutum (20), and the mesepisternum (25) have moderate scores for this factor. However the four characters from the clypeus (3), the first metasomal tergum (38), the third metasomal tergum (41), and the third metasomal sternum (48) have low scores for the factor with the value of -0.16, -0.21, -0.39 and -0.24, respectively. Therefore the strength of punctures of the clypeus and the metasoma have their independent variation of the general roughness of the integument. When this character direction is highly developed, it will cause to produce a rough integument in places of the body.

Fifth character association (Fig. 5) affected by Factor V is *the size of punctures on the clypeus* (2, 0.87), *the strength of punctures on the clypeus* (3, 0.86), *the puncture density of the clypeus* (4, 0.81), *the strength of the fro&al line* (7, 0.69), *the size of punctures on the mesoscutum* (19, 0.50), and *the size of the propodeal enclosure* (27, -0.71). According to the consideration in the Factor I and IV, the density and strength of punctures on the clypeus also seem to have their own variation. The present result supports it. This factor seems to have some connection with the punctation of the clypeus with the exception of the size of the propodeal enclosure. Three characters of the punctation of the clypeus (2, 3, and 4) mutually have considerably high correlations with the value of 0.69 to 0.80. Observation on the matrix shows that the size of the propodeal enclosure (27) has moderate negative correlations with the various characters such as the size of punctures on the clypeus (-0.49), the puncture density of the vertex (-0.50), and the strength of the hypostomal carina (-0.49). If the character group is well developed, it will probably lead to a construction of a

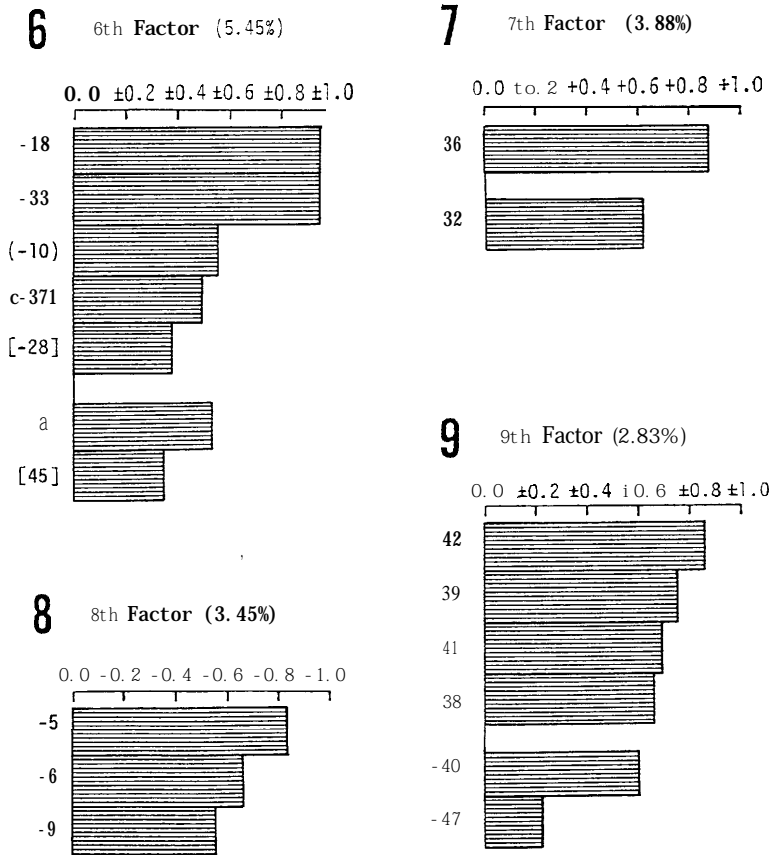


Figs. 4 and 5. Factor loadings of higher loading sculpture characters for the 4th and 5th common factors extracted by factor analysis with varimax rotation.

large, strongly, much punctured clypeus.

Sixth character group (Fig. 6) which has highest negative and positive loadings for Factor VI includes *the existence of lateral lugulae of the pronotum* (18, -0.94), *the existence of lateral keels on the dorso-lateral face of the propodeum* (33, -0.94), *the strength of punctures on the genal area* (10, -0.54), *the curvature of the posterior spurs on the hind tibiae* (37, -0.49) and *the strength of lugulae on the upper paraocular areas* (8, 0.53). Although some characters have moderate scores for this factor the two wrinkled characters of the different regions, the lateral pronotum (18) and the lateral propodeum (33), have strongly high scores for it. Therefore it is reasonable that the Factor IV is concerned with the wrinkles of the lateral thorax.

Seventh character group (Fig. 7) holding highest loadings for Factor VII is composed of *the existence of spines near apex of the hind femur* (36, 0.88), *the curvature of posterior spurs on the hind tibiae* (37, 0.49), and *the tessellation of the dorsal face of the propodeum* (32, -0.62). The spine character of the hind femur has



Figs. 6-9. Factor loadings of higher loading sculpture characters for the 6th to the 9th common factors extracted by factor analysis with varimax rotation.

a relatively low negative correlation with the tessellation of the dorsal face of the propodeum with the value of -0.39. Judging from the strong loading for the character, the present consideration treats this factor as the index of the spines of the hind femur.

Eighth character group (Fig. 8) holding highest negative loadings for Factor VIII consists of **the degree of separation of the facial fovea from the eye margin** (5, -0.85), **the depth of the facial fovea** (6, -0.67) and **the puncture density of vertex** (9, -0.57). Although this factor includes mixed characters, the first two characters derived from the facial fovea have the correlation value of 0.56 with each other, while they have the value of 0.46 and 0.37 with the puncture density of the vertex, respectively. Adopting the characters holding higher loadings as the preceding group, the present factor is considered as the distinctness of the facial fovea. When this character association is developed, it will lead to a formation of deep facial fovea separated from eye margin,

Ninth character group (Fig. 9) which has highest loadings for Factor IX is composed of the following characters. *The puncture density of the third metasomal tergum* (42, 0.87), *the puncture density of the first metasomal tergum* (39, 0.76), *the strength of punctures on the third metasomal tergum* (41, 0.70), and *the strength of punctures on the first metasomal tergum* (38, 0.67), and *the tessellation of the first metasomal tergum* (40, -0.62). This factor is obviously concerned with the punctation of the metasomal terga. Observation on the matrix shows that the above four puncture characters of the metasomal terga (38, 39, 41 and 42) have high correlations with one another. The highest correlation is obtained between the strength and density of punctures on the first tergum with the value of 0.76. The lowest correlation is obtained between the strength of punctures on the first tergum and the density of punctures on the third tergum with the value of 0.55. These four characters have relatively low correlations with the strength of punctures on the third metasomal sternum (48) with 0.38 to 0.55. On the other hand, they have moderate to high negative correlations with the tessellation of the first (40) and the third (43) metasomal terga with -0.26 to -0.64.

The remaining characters excluded in the above groupings are as follows: *the existence of the longitudinal impunctate line on the clypeus* (1), *the curvature of the hypostomal carina* (12), *the existence of emargination on antero-medial portion on the pronotum* (17), *the distinctness of boundary of the propodeal enclosure* (28), *the width of posterior depression of the third metasomal tergum* (45), *the distinctness of triangular area of the pygidial plate* (47), *the strength of punctures on the third metasomal sternum* (48), and *the number of graduli on the metasomal sterna* (50). Among these characters, the character coded 17 is connected with the special Factor X, the character 12 is concerned with the special Factor XI, the characters 1 and 47 are related to the special Factor XII. The character coded 48 has some connection with the special Factor XIII. They are considered to have their own independent variations of the other characters.

The character profiles are further observed by examining the factor scores of OTU's for the common factors (Table 4).

The Factor I has its highest negative loadings on OTU's *valeriana* (35, -2.5), *ishikuwai* (36, -1.6), *Andrena* sp. 2 (67, -1.6), *Andrena* sp. 3 (68, -1.6), *takachioi* C (72, -1.5) and its highest positive loadings on OTU's *hikosana* (42, 2.3), *prostomias* (14, 1.9), *brassicae* (43, 1.9), *maetai* (22, 1.8), *miyamotoi* (39, 1.8), *sublevigata* (46, 1.8), *richardsi* (51, 1.8), *echizenia* (63, 1.8), *fukuiana* (64, 1.8), *knuthi* (19, 1.5) and *knuthi okinawana* (20, 1.5). Although the factor is strongly loaded on the two characters of the puncture density on the thorax, the result is not necessarily manifested in the negative scores for the OTU's. On the other hand, concerning the positive scores, it becomes clear that the OTU's holding higher ones show the mesoscutum and the scutellum sparsely punctured. Therefore the factor is considered to be as "the sparseness of

Table 4. Factor scores of 85 OTU's of the Japanese andrenid bees for the nine common factors derived from 50 characters of integumental sculptures.

| OTU name | Factor scores | | | | | | | | |
|--|---------------|--------|--------|--------|--------|---------|--------|--------|--------|
| | I | II | III | IV | V | VI | VII | VIII | IX |
| 1 <i>brevihirtiscopa</i> | 1.151 | -1.875 | 0.291 | 0.681 | 0.725 | -3.960 | -0.483 | -0.169 | 0.080 |
| 2 <i>mikado</i> A | -0.893 | -1.797 | 0.522 | 0.394 | 0.253 | 0.010 | -0.127 | 0.741 | 0.332 |
| 3 <i>bombiformis</i> | 0.008 | -1.944 | 0.600 | 0.536 | 0.033 | -0.420 | -0.514 | 0.725 | 0.599 |
| 4 <i>ishiharai</i> | -0.805 | -1.685 | -0.003 | 0.383 | 0.407 | 0.496 | -0.202 | 0.872 | 0.635 |
| 5 <i>nawai</i> | 0.154 | -1.992 | 0.818 | 0.685 | 0.810 | -0.924 | -0.448 | 0.504 | 0.570 |
| 6 <i>esakii</i> | 0.202 | -1.148 | 0.328 | -0.245 | 0.005 | -0.102 | -0.060 | 1.395 | 0.201 |
| 7 <i>longitibialis</i> | -0.360 | -1.388 | -0.108 | -0.135 | -0.102 | 2.540 | -0.097 | 0.984 | -0.460 |
| 8 <i>maukensis</i> | -0.119 | -1.662 | 0.131 | -0.059 | 0.299 | -0.342 | -0.093 | 0.714 | -1.006 |
| 9 <i>shirozui</i> | -0.553 | -1.400 | 0.473 | -0.135 | -0.169 | 1.288 | 0.103 | 0.972 | -1.158 |
| 10 <i>hondoica</i> | 0.558 | -1.168 | 0.589 | 0.240 | 0.010 | 2.622 | -0.319 | 0.808 | -0.680 |
| 11 <i>aburana</i> | 0.470 | -1.567 | -0.658 | -0.056 | 0.365 | 0.943 | -0.057 | 0.945 | -0.491 |
| 12 <i>saragamineensis</i> | -0.595 | -1.121 | -0.278 | 0.075 | -0.047 | 1.931 | -0.197 | 0.576 | -0.554 |
| 13 <i>benefica</i> | 0.761 | -1.448 | -1.698 | 0.038 | 0.739 | -0.279 | 0.348 | 0.301 | -0.659 |
| 14 <i>prostomias</i> | 1.883 | -0.064 | 0.758 | -0.076 | -1.195 | -0.547 | 0.340 | -0.457 | 1.457 |
| 15 <i>tsukubana</i> | 0.435 | 0.434 | 0.426 | -0.012 | -1.204 | 1.548 | 0.131 | -0.727 | 0.863 |
| 16 <i>mitakensis</i> | 0.787 | 0.078 | 0.913 | 0.625 | 0.673 | -1.716 | 0.613 | -2.856 | 0.431 |
| 17 <i>kamikochiana</i> | 0.187 | 0.533 | 0.931 | 0.507 | -0.919 | 2.321 | 0.255 | -1.003 | -0.072 |
| 18 <i>taraxaci</i> <i>chikuzenensis</i> | -1.341 | 0.073 | -0.309 | -0.133 | 0.537 | -0.795 | 3.905 | 1.043 | 0.254 |
| 19 <i>knuthi</i> | 1.531 | 0.831 | 0.095 | -0.376 | -0.420 | 2.035 | 4.924 | 0.044 | 0.080 |
| 20 <i>knuthi okinawana</i> | 0.445 | 0.479 | 0.475 | -0.111 | -0.825 | 0.556 | 4.897 | 0.422 | 0.724 |
| 21 <i>seneciorum</i> | 1.503 | -0.242 | -1.003 | -0.110 | 1.360 | 1.069 | -0.422 | -0.716 | -0.669 |
| 22 <i>maetai</i> | 1.793 | -1.700 | 0.010 | 0.393 | 0.617 | -0.960 | -0.116 | -1.268 | 0.818 |
| 23 <i>albicaudata</i> | 1.113 | -0.831 | -0.927 | 0.294 | 0.642 | 1.854 | -0.008 | -0.932 | 0.292 |
| 24 <i>hebes</i> | -1.117 | 0.037 | -0.169 | 0.442 | 0.480 | 1.202 | 0.176 | -1.149 | -1.142 |
| 25 <i>stellaria</i> | -0.004 | 0.293 | 0.554 | 0.222 | 0.521 | 0.920 | -0.208 | -0.744 | -1.459 |
| 26 <i>ruficrus rabricrus</i> | -0.416 | -0.822 | 0.338 | 0.942 | 1.403 | -3.299 | 0.432 | -2.124 | -0.791 |
| 27 <i>takachioi</i> A | -0.647 | 0.021 | 1.473 | 0.946 | 1.172 | 0.692 | -0.082 | -1.184 | -0.640 |
| 28 <i>watasei</i> | 0.282 | 1.455 | 0.834 | 0.400 | 1.526 | -0.033 | -0.304 | 0.106 | 1.412 |
| 29 <i>wulungshanensis</i> | 0.734 | 2.375 | 1.747 | -0.215 | 1.033 | 1.990 | -1.267 | -0.745 | -0.020 |
| 30 <i>parat horacica</i> | 0.018 | 1.993 | 0.845 | 0.290 | 1.129 | 1.830 | -0.052 | 0.284 | 1.119 |
| 31 <i>okabei sapporensis</i> | -0.742 | 1.541 | 0.898 | 0.862 | 1.891 | -0.585 | -0.076 | 0.197 | 1.572 |
| 32 <i>edashigei</i> A | -0.453 | 0.198 | 0.842 | 0.548 | 0.763 | 0.990 | 0.292 | -0.835 | 1.268 |
| 33 <i>sasakii</i> | 0.742 | 0.529 | -0.539 | 0.555 | 0.747 | 2.362 | -0.224 | -0.515 | 0.648 |
| 34 <i>omogensis</i> | 0.934 | -0.110 | 1.226 | 0.087 | -1.406 | -1.406 | 0.729 | 0.951 | 1.315 |
| 35 <i>valeriana</i> | -2,457 | 1.702 | -2.359 | 1.577 | -0.194 | -13.544 | -0.390 | -0.117 | -0.320 |
| 36 <i>ishikawai</i> | -1.639 | 0.897 | -0.945 | 1.285 | -1.548 | -12.408 | 0.680 | -0.105 | -1.168 |
| 37 <i>taniguchiaie</i> | -1.443 | 0.530 | -1.848 | 1.262 | -0.867 | -14.867 | -0.134 | -0.509 | -0.927 |
| 38 <i>dentata</i> | 1.111 | 0.585 | -2.161 | 0,366 | 1,730 | -0.129 | 0,193 | 0.007 | -0.658 |
| 39 <i>miyamotoi</i> | 1.797 | 0.455 | 0.279 | 0.609 | 1.166 | -1.194 | -0.373 | 0.809 | -1.558 |
| 40 <i>sachalinensis</i> | 1.032 | 0.574 | -1.475 | 0.551 | 1.547 | -0.172 | -0.476 | 0.634 | 0.190 |
| 41 <i>pruniphora</i> | 0.085 | 0.692 | -2.261 | 0.626 | 1.461 | 0.900 | -0,133 | -0.751 | -0.041 |
| 42 <i>hikosana</i> | 2.345 | 0.281 | -0.759 | -0.621 | -1.335 | -0.308 | -1.078 | -1.832 | 0.698 |
| 43 <i>brassicae</i> | 1.926 | 0.113 | -0.139 | -0.412 | -1.337 | -1.551 | -0.434 | 0.254 | -1.139 |
| 44 <i>kaguya</i> A | -0.269 | 0.325 | -1.371 | -0.311 | -1.632 | 1.598 | -0.618 | -0.644 | -1.607 |
| 45 <i>komachi</i> A | -1.026 | 0.784 | -2.231 | -0.543 | -1.485 | 1.645 | -0.259 | -0.819 | 0.058 |

Table 4. Continued.

| OTU name | Factor scores | | | | | | | | |
|------------------------------------|---------------|--------|--------|--------|--------|--------|--------|--------|--------|
| | I | II | III | IV | V | VI | VII | VIII | IX |
| 46 <i>sublevigata</i> | 1.827 | 0.474 | 0.550 | -0.404 | -1.704 | 2.600 | -0.753 | 0.952 | -1.682 |
| 47 <i>falsificissima</i> | -1.130 | 0.741 | -2.525 | -1.090 | -1.898 | 3.829 | -0.284 | 0.381 | 0.021 |
| 48 <i>japonica</i> | -0.281 | 0.190 | 0.436 | -4.463 | 0.052 | 5.121 | -0.716 | -0.167 | 0.761 |
| 49 <i>fukaii</i> | -0.659 | 0.235 | 0.637 | -4.028 | 0.954 | 0.741 | -0.505 | 0.080 | 0.214 |
| 50 <i>nitidiuscula</i> | 0.736 | -0.937 | 1.218 | 0.882 | -0.679 | 0.799 | -0.293 | -0.001 | 0.813 |
| 51 <i>richardsi</i> | 1.774 | -0.373 | -0.096 | -0.018 | -1.064 | 1.581 | -0.869 | -0.107 | 1.408 |
| 52 <i>amamiensis</i> | -1.264 | -0.845 | -0.494 | 0.144 | -1.309 | 0.670 | 0.429 | -2.494 | 1.842 |
| 53 <i>yasumatsui</i> | 0.943 | -0.964 | -0.760 | 0.366 | -1.485 | 1.191 | 0.395 | -0.586 | 1.463 |
| 54 <i>astragalina</i> | 0.343 | 1.150 | 0.446 | -3.330 | 1.823 | -0.654 | 1.251 | 2.093 | -0.514 |
| 55 <i>fukuokensis</i> | -1.181 | 0.006 | -0.380 | 0.071 | -1.125 | 0.111 | 0.428 | 0.416 | 1.306 |
| 56 <i>opacifovea</i> | 0.056 | -0.228 | 0.314 | -0.471 | -0.240 | -3.202 | -1.114 | 1.475 | 1.266 |
| 57 <i>kerriae</i> | -1.291 | 0.287 | -1.078 | 0.020 | -0.753 | -0.356 | -0.771 | 1.557 | 2.565 |
| 58 <i>halictoides</i> | 0.778 | -1.253 | 1.143 | 0.520 | -0.824 | -1.429 | 0.117 | 0.133 | 0.829 |
| 59 <i>ezoensis</i> | -0.330 | -0.032 | 3.444 | 0.208 | 1.285 | -0.476 | 0.230 | -0.742 | 1.040 |
| 60 <i>foveopunctata</i> | -0.274 | -1.699 | 0.758 | -3.808 | 0.834 | 0.153 | -0.131 | -2.229 | -0.376 |
| 61 <i>haemaphysalis japonica</i> | -0.957 | -0.388 | 0.301 | -2.909 | 0.723 | 1.291 | -0.282 | -1.861 | 0.461 |
| 62 <i>coitana pilosodorsata</i> | 0.975 | 0.605 | 1.279 | 0.625 | -0.154 | -0.558 | -0.083 | -1.127 | -0.623 |
| 63 <i>echizenia</i> | 1.759 | 1.318 | 0.683 | -0.246 | 0.284 | 1.979 | 0.151 | 0.984 | -1.189 |
| 64 <i>fukuiana</i> | 1.833 | 0.772 | 0.394 | -0.371 | 0.085 | 2.118 | 0.087 | 1.021 | -1.045 |
| 65 <i>mikado</i> B | -0.897 | -1.680 | 0.402 | 0.360 | 0.074 | 1.345 | -0.108 | 0.687 | 0.216 |
| 66 <i>Andrena</i> sp. 1 | 0.081 | -1.787 | 0.783 | 0.185 | 0.031 | 0.463 | 0.138 | 0.636 | -0.388 |
| 67 <i>Andrena</i> sp. 2 | -1.596 | 0.216 | 1.080 | 0.423 | -0.166 | 0.028 | 0.233 | 1.124 | 0.372 |
| 68 <i>Andrena</i> sp. 3 | -1.531 | -0.981 | 0.630 | 0.222 | -0.258 | 2.300 | 0.071 | 0.859 | -0.926 |
| 69 <i>Andrena</i> sp. 4 | 1.201 | -0.125 | -0.668 | -0.253 | 0.494 | 3.095 | 0.367 | 0.767 | -1.024 |
| 70 <i>Euandrena</i> sp. 1 | -0.581 | 0.326 | -0.553 | 1.023 | -0.015 | 0.746 | -0.422 | -0.251 | 0.857 |
| 71 <i>takachihoi</i> B | -0.938 | 0.541 | 1.124 | 0.894 | 0.971 | 2.541 | -0.162 | -0.959 | -0.579 |
| 72 <i>takachihoi</i> C | -1.485 | 0.062 | 1.537 | 1.075 | 0.690 | 0.771 | -0.258 | -0.669 | -0.695 |
| 73 <i>takachihoi</i> D | -0.527 | -0.216 | 1.284 | 0.900 | -0.122 | 0.245 | -0.443 | -0.527 | 0.165 |
| 74 <i>edashigei</i> B | -0.451 | 0.805 | 0.660 | 0.509 | 0.784 | 1.297 | -0.034 | -0.353 | 1.699 |
| 75 <i>Hoplandrena</i> sp. 1 ssp. 1 | -0.563 | -0.341 | -1.683 | 0.343 | 1.165 | -1.617 | 0.282 | 0.210 | -1.010 |
| 76 <i>Hoplandrena</i> sp. 1 ssp. 2 | -1.305 | 1.030 | -0.321 | 0.336 | 1.147 | 1.135 | -0.016 | 1.122 | -1.929 |
| 77 <i>Micrandrena</i> sp. 1 | -1.210 | 1.130 | -1.160 | 0.028 | -1.633 | 0.656 | 0.214 | -0.662 | -1.230 |
| 78 <i>Micrandrena</i> sp. 2 | -0.942 | 1.480 | 0.382 | -0.113 | -1.624 | -1.893 | -0.411 | -0.208 | -0.466 |
| 79 <i>Micrandrena</i> sp. 3 | 0.314 | 0.543 | 0.333 | -0.093 | -1.649 | 1.116 | -0.538 | -0.174 | -1.563 |
| 80 <i>Micrandrena</i> sp. 4 | -1.197 | 0.877 | 0.510 | 0.006 | -1.299 | -2.068 | -0.231 | -0.371 | -1.463 |
| 81 <i>komachi</i> B | -0.540 | 0.830 | -0.253 | -0.468 | -1.598 | -1.607 | -0.546 | 0.407 | -0.453 |
| 82 <i>kaguya</i> B | -0.988 | 0.761 | 1.434 | 0.340 | -1.192 | -1.181 | -0.393 | -0.525 | -1.857 |
| 83 <i>Simandrena</i> sp. 1 | 1.045 | 1.351 | -0.322 | -0.093 | -0.052 | 0.471 | -1.640 | 1.892 | 1.188 |
| 84 <i>Simandrena</i> sp. 2 | -0.084 | 0.752 | 0.695 | 0.379 | 0.600 | 1.692 | -1.309 | 1.546 | 1.654 |
| 85 <i>Simandrena</i> sp. 3 | -0.531 | 1.522 | -0.430 | -0.572 | -0.503 | 0.768 | -0.827 | 1.585 | 0.549 |

punctures on the thorax".

The Factor II has its highest negative loadings on OTU's *nawai* (5, -2.0), *brevihirtiscopea* (1, -1.9), *bombiformis* (3, -1.9), *mikado* A (2, -1.8), *Andrena* sp.

1 (66, -1.8), *ishiharai* (4, -1.7), *esakii* (6, -1.7), *maetai* (22, -1.7), *foveopunctata* (60, -1.7), *mikado* B (65, -1.7), *longitibialis* (7, -1.6) and its highest positive loadings on OTU's *wulungshanensis* (29, 2.4), *parathoracica* (30, 2.0), *valeriana* (35, 1.7), *watasei* (28, 1.5), *okabei sapporensis* (31, 1.5), *Micrandrena* sp. 2 (78, 1.5) and *Simandrena* sp. 3 (85, 1.5). Although the preceding consideration on the Factor II does not sufficiently lead to interpreting it, this result suggests that the factor is concerned with "the pronotal suture or humeral angle on the pronotum". Because the OTU's of the subgenus *Andrena*, which have highest negative scores, show strong indication of the humeral angle and weak indication of the pronotal suture. On the other hand, the OTU's of the subgenus *Gymnandrena*, which have highest positive scores, show weak indication of the humeral angle and strong indication of the pronotal suture. The subgenera *Andrena* and *Gymnandrena* are characterized by this factor with respect to the integumental sculpture.

The Factor III has its highest negative loadings on OTU's *ezoensis* (59, -3.4), *falsificissima* (47, -2.5), *valeriana* (35, -2.4), *pruniphora* (41, -2.3), *dentata* (38, -2.2), *komachi* A (45, -2.2), *taniguchiae* (37, -1.8), *benefica* (13, -1.7), *Hoplendrena* sp. 1 ssp. 1 (75, -1.7), *sachalinensis* (40, -1.5), and its highest positive loadings on OTU's *wulungshanensis* (29, 1.7), *takachihoi* A (27, 1.5) and *takachihoi* C (72, 1.5). The above OTU's of the subgenera *Taenandrena*, *Micrandrena*, *Hoplendrena* and *Andrena* which hold highest negative scores have densely tessellate metasoma. The factor is considered to be associated with "the development of tessellation on the metasoma" with the exception of two OTU's of the subgenus *Holandrena*.

The Factor IV has its highest negative loadings on OTU's *japonica* (48, -4.5), *fukaii* (49, -4.0), *foveopunctata* (60, -3.8), *astragalina* (54, -3.3), *haemorrhoea japonibia* (61, -2.9), and its highest positive loading on OTU *valeriana* (35, 1.6). From the result it is obvious to regard this factor as "the roughness of the integument". Because the above OTU's also show rough integument such as a carina and wrinkles on the propodeal enclosure, and reflections on the posterior margins of the metasomal terga. The more an OTU has negative scores, the rougher the integument of it will be. It may be considered that this factor is helpful in distinguishing the subgenera *Mitsukurilla*, *Trachandrena*, and *Plastandrena* from the other subgenera.

The Factor V has its highest positive loadings on OTU's *okabei sapporensis* (31, 1.9), *astragalina* (54, 1.8), *dentata* (38, 1.7), *watasei* (28, 1.5), *sachalinensis* (40, 1.5), and *pruniphora* (41, 1.5), and its highest negative loadings on OTU's *falsificissima* (47, -1.9), *sublevigata* (46, -1.7), *kaguya* A (44, -1.6), *Micrandrena* sp. 1 (77, -1.6), *Micrandrena* sp. 2 (78, -1.6), *Micrandrena* sp. 3 (79, -1.6) and *komachi* B (81, -1.6). The above OTU's holding highest positive scores have the clypeus strongly, largely, and densely punctured, and the propodeal enclosure smaller for the size of insect. On the other hand, the OTU's holding

highest negative scores have the converse states of characters. The factor is considered to be as "the development of punctation on the clypeus and the size of the propodeal enclosure". The subgenus *Micrandrena* is well characterized by this factor.

The Factor VI has its highest negative loadings on OTU's *taniguchiae* (37, -14.9), *valeriana* (35, -13.2), *ishikawai* (36, -12.4). These OTU's have the lateral lugulae on the pronotum and the lateral keel on the dorsal face of the propodeum. Therefore the factor seems to be "the appearance of wrinkles of the lateral thorax". The subgenus *Holandrena* is best distinguished by this factor.

The Factor VII has its highest positive loadings on OTU's *knuthi* (19, 4.9), *knuthi okinawana* (20, 4.9), and *taraxaci chikuzenensis* (18, 3.9). These OTU's have a row of short spines near apex of the hind femur. Judging from the high scores for these OTU's, the factor seems to be "the appearance of spines on the hind femur". The subgenus *Chlorandrena* is nicely characterized by this factor.

The Factor VIII has its highest negative loadings on OTU's *mitakensis* (16, -2.9), *amamiensis* (52, -2.5), *foveopunctata* (60, -2.2), *ruficrus rabicrus* (26, -2.1), *haemorrhoea japonibia* (61, -1.9), and *hikosana* (42, -1.8), and its highest positive loadings on OTU's *astragalina* (54, 2.1), *Simandrena* sp. 1 (83, 1.9), *kerriae* (57, 1.6), *Simandrena* sp. 3 (85, 1.6), *opacifovea* (56, 1.5), and *Simandrena* sp. 2 (84, 1.5). The above OTU's holding highest negative scores also show the facial fovea deeply indicated and widely separated from the eye margin, while the OTU's holding highest positive scores indicate the inverse states of characters. So this factor considered to be "the distinctness of the facial fovea". The OTU's of the subgenus *Trachandrena* are characterized by this factor.

The Factor IX has its highest positive loadings on OTU's *kerriae* (57, 2.6), *amamiensis* (52, 1.8), *edashigei* B (74, 1.7), *okabei sapporensis* (31, 1.6), *Simandrena* sp. 2 (84, 1.6), *prostomias* (14, 1.5), and *yasumatsui* (53, 1.5), and its highest negative loadings on OTU's *Hoplendrena* sp. 1 ssp. 2 (76, -1.9), *kaguya* B (8.2, -1.9), *sublevigata* (46, -1.7), *miyamofoi* (39, -1.6), *kaguya* A (44, -1.6), and *Micrandrena* sp. 3 (79, -1.6). The OTU's holding highest positive scores have the metasomal terga densely and strongly punctate such as in *kerriae* and *amamiensis*. On the other hand, the negative group has the metasomal terga densely tessellate. The factor is considered to be "the development of punctation on metasomal terga".

The interpretation of the common factors is summarized as follows: the Factor I as the sparseness of punctures on the thorax, the Factor II as the development of the suture or angle on the pronotum, the Factor III as the development of tessellation on the metasoma, the Factor IV as the roughness of integument, the Factor V as the development of punctation on the clypeus, the Factor VI as the appearance of wrinkles on the lateral thorax, the Factor

VII as the appearance of spines on the hind femur, the Factor VIII as the distinctness of the facial fovea, and the Factor IX as the development of punctation on the metasomal terga.

Since the characters are correlated as mentioned above, it is possible to describe most of the phenetic variation in terms of much fewer factors. The present study showed that 73.08 percent of the total variance was accounted for by the first nine factors. The biological interpretation of the factors was relatively easy. This is because the characters employed were restricted to the surface sculptures. It is possible to imagine that most character associations extracted are structurally related. The analysis also reveals clearly that the similar characters such as punctation and tessellation are not necessarily affected by the same common factors throughout the body. They have their own character variations with respect to the regions of the body. It is also of interest that the analysis extracted the specialized character association which characterizes a certain subgenus. For instance the wrinkles on the lateral thorax related with the sixth factor characterizes the subgenus *Hopl-andrena*, and the spines on the hind femur related with the seventh factor distinguishes the subgenus *Chlorandrena*. The result suggests that specialized character association used for the taxonomy is also able to be extracted in the factor analysis. By delimiting structural or functional complexes, the factor analysis provides a useful data synthesis capable of suggesting causal relations. It may be expected that these correlation analysis based on small samples would be needful before extensive character data are gathered for a final systematic study.

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