

An Approach to the Revision of the East Asian Millipede Genus *Anaulaciulus*

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ABSTRACT

The millipede genus *Anaulaciulus* Pocock, 1895 (Julida: Julidae) comprises 44 species, distributed in Eastern Asia. Based on fresh studies of numerous samples, type material and literature, a comprehensive overview of the genus is proposed. A list of the presently known species is given, and a preliminary grouping is outlined on the basis of their posterior gonopod structure. Other external and internal characters, such as penis, gonopod promerit and female vulva structure, coloration, size, and shape of the preanal projection are discussed and evaluated. Two examples of evolutionary gonopod transformation series are presented and illustrated.

RÉSUMÉ

Essai de révision du genre est-asiatique *Anaulaciulus*.

Le genre *Anaulaciulus* Pocock, 1895 (Diplopoda, Julida, Julidae) comprend 44 espèces réparties dans l'Est asiatique. La présente révision, basée sur l'examen récent de nombreux exemplaires, permet de présenter une liste dans laquelle les espèces sont séparées en groupes provisoirement basés sur la structure des gonopodes postérieurs. D'autres caractères, externes et internes, tels que le pénis, le promérite des gonopodes, la structure des vulves, la coloration, la taille, et la forme du telson sont discutés et évalués. Deux exemples de transformation évolutive des gonopodes sont présentés et illustrés.

INTRODUCTION

The genus *Anaulaciulus* at present consists of 44 nominal species (with 4 proposed subspecies) including 10 forms recently described from the Southern Himalaya region (KORSÓS, in press). Part of the original descriptions of the other species are rather old and not properly detailed, type material of those is usually difficult to obtain. As the range of the genus (see below) implies, there may certainly be a large number of yet undiscovered species. However, considering the available material, a preliminary review of the genus seems not to be premature.

The distribution of the species in the genus includes the temperate zone of Eastern Asia: from Pakistan to the Russian Far East, through Nepal, northern India, Sikkim, Tibet, northeastern China and Korea, including Hong-Kong and Taiwan. Numerous forms occur also in Japan, south of Hokkaido (Honshu, Shikoku, Kyushu, Ryukyu Islands, Bonin Islands). To the contrast of the other widespread Eastern Asian julid genus *Nepalmatoiulus*, *Anaulaciulus*

KORSÓS, Z., 1996. — An approach to the revision of the East Asian millipede genus *Anaulaciulus*. In: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 35-43, Paris ISBN : 2-85653-502-X.

does not seem to penetrate into the tropical regions, it is confined to the temperate zone or high altitudes.

The genus name itself was introduced by POCOCK in 1895, and subsequently generally overlooked. The majority of the species belonging now to *Anaulaciulus* were originally described in *Fusiulus* Attems, 1909, and only in 1966 did CAUSEY recognize the synonymy with a redescription of the two POCOCK's species (*paludicola* and *vallicola*).

Anaulaciulus belongs in the tribe Brachyiulini, which can be characterized as follows:

Julidae (Brachyiulinae) without a free mesomerit on the posterior gonopod, with a well-developed flagellum, and generally compressed gonopods in the antero-posterior direction. About 24 genera are enlisted in this tribe, however, their relationship has not yet been completely clarified.

The genus *Anaulaciulus* can be defined on the basis of some peculiarities externally as well as in the gonopod conformation. The animals have no metazonal setae, no cheek lobes expanded in the males. Male gonopod promerites are characteristically flattened, scale-like, a rudiment of the telopodit is well visible. Posterior gonopods are rather simple, elongated, *in situ* always protruding from beneath protecting promerites, and have several longitudinal, slightly arched lamellae. The penis is long, bifurcate in every species; this character seems to be a unique apomorphy for the genus in the entire millipede order Julida; even the closest relatives of the genus in the tribe Brachyiulini have a completely different penis (Figs 1-3). The long, leaf-like structure (differently developed in the different species) seems to be homologous with the apical membrane in the other species, and the opening of the seminal groove is situated most probably caudally at the basis of the "leaves".

The female vulval characters show also some peculiarities as compared to other members of the tribe. They are slightly compressed in the antero-posterior direction (others are more-or-less cylindrical), the well-separated operculum is always longer than bursa and apically provided with two lateral cusps (often also a median one). The median cleft on bursa is deep, the apodemetic tube without secondary branches, the ampulla usually without an appendix.

A more detailed characterization of the genus is given elsewhere (KORSÓS, in press).

There are very few works devoted to a summary or clarification of the internal relationships of *Anaulaciulus*. An identification key is given to the species known at that time by VERHOEFF, first in 1937 (for five species), then in 1941 (for 9 species, VERHOEFF, 1941a), and by TAKAKUWA (1941, for 16 forms). They are all based mainly on minor gonopodal character details, and not very useful, especially if one regards the different quality of the descriptions and the possible morphological variations in the populations. ENGHOFF (1986) lists 28 nominal species and 6 subspecies with comments on their distribution. He establishes the synonymies of *A. ciliatus* Shinohara, 1960 and *F. trilobus quemoyensis* Wang, 1963. Apart from these, no attempt for the revision of the entire genus has been made.

REVIEW OF THE SPECIES

In the followings, a renewed alphabetical list of the presently known species in the genus is given, together with a name history and distributional data of every species. Illustrations wherever available are also referred to.

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|--|----------------|
| 1. <i>Anaulaciulus acaudatus</i> Korsós, in press
<i>Anaulaciulus acaudatus</i> : KORSÓS, in press (FIGS 26-28) | India: Sikkim. |
| 2. <i>Anaulaciulus acutus</i> (Takakuwa, 1941)
<i>Fusiulus acutus</i> : TAKAKUWA, 1941 (FIGS 2-3)
<i>Anaulaciulus acutus</i> : ENGHOFF, 1986 | Japan: Honshu. |
| 3. <i>Anaulaciulus attemsii</i> (Verhoeff, 1941)
<i>Fusiulus attemsii</i> : VERHOEFF, 1941a (FIGS 31-33)
<i>Anaulaciulus attemsii</i> : ENGHOFF, 1986 | Japan: Honshu. |

4. **Anaulaciulus bilineatus** Korsós, in press
Anaulaciulus bilineatus: KORSÓS, in press (FIGS 2-4, 6, 9, 11, 29-33) Nepal.
5. **Anaulaciulus bilobus** (Takakuwa, 1941)
Fusiulus bilobus: TAKAKUWA, 1941 (FIGS 10-11)
Anaulaciulus bilobus: ENGHOFF, 1986 Japan: Kyushu.
6. **Anaulaciulus capillatus** (Takakuwa, 1941)
Fusiulus capillatus: TAKAKUWA, 1941 (FIGS 12-13)
Anaulaciulus capillatus: ENGHOFF, 1986 Japan: Honshu.
7. **Anaulaciulus cornutus** (Takakuwa, 1941)
Fusiulus cornutus: TAKAKUWA, 1941 (FIGS 17-18)
Anaulaciulus cornutus: ENGHOFF, 1986 Japan: Kyushu.
8. **Anaulaciulus enghoffi** Korsós, in press
Anaulaciulus enghoffi: KORSÓS, in press (FIGS 34-41) China: Kansu.
9. **Anaulaciulus golovatchi** Mikhajlova, 1982
Anaulaciulus golovatchi: MIKHAILOVA, 1982 (FIG. 2)
Anaulaciulus golovatchi: ENGHOFF, 1986 Russia: Far East, Maritime Province; recently reported from North Korea as well (MIKHAILOVA, 1993).
10. **Anaulaciulus hirosaminus** (Attems, 1909)
Fusiulus hirosaminus: ATTEMS, 1909 (FIGS 76-78)
Anaulaciulus hirosaminus: ENGHOFF, 1986 Japan: Hiro Sami.
11. **Anaulaciulus inaequipis** Enghoff, 1986
Anaulaciulus inaequipis: ENGHOFF, 1986 (FIGS 1-4)
Anaulaciulus inaequipis: KORSÓS, in press (FIGS 20-25) Burma.
12. **Anaulaciulus kashmirensis** Korsós, in press
Anaulaciulus kashmirensis: KORSÓS, in press (FIGS 42-47) India: Kashmir.
13. **Anaulaciulus kiusiensis** (Verhoeff, 1941)
Fusiulus kiusiensis: VERHOEFF, 1941a (FIGS 34-36)
Anaulaciulus kiusiensis: ENGHOFF, 1986 Japan: Kyushu.
14. **Anaulaciulus komatsui** (Shinohara, 1957)
Fusiulus komatsui: SHINOHARA, 1957 in TAKAKUWA & SHINOHARA, 1957 (FIG. 2)
Anaulaciulus komatsui (Takakuwa & Shinohara, 1957): ENGHOFF, 1986 Japan: Honshu.
15. **Anaulaciulus koreacolus** Jedryczkowski, 1982
Anaulaciulus koreacolus: JEDRYCZKOWSKI, 1982 (FIGS 28-36)
Anaulaciulus koreacolus: ENGHOFF, 1986 Korea: Sunchon and Hyangsan districts.
16. **Anaulaciulus koreanus** (Verhoeff, 1937)
Fusiulus koreanus: VERHOEFF, 1937 (FIGS 4-8)
Fusiulus koreanus koreanus Verhoeff, 1937: PAIK, 1976
Anaulaciulus koreanus: ENGHOFF, 1986
Anaulaciulus koreanus koreanus: LIM, 1988 Korea: Hoko.
- 16.1. **Anaulaciulus koreanus boninensis** (Verhoeff, 1939)
Fusiulus koreanus boninensis: VERHOEFF, 1939a (FIGS 16-17)
Anaulaciulus koreanus boninensis: GOLOVATCH, 1980 (FIGS 1-2)
Anaulaciulus koreanus boninensis: ENGHOFF, 1986 Japan: Bonin Islands, Ryukyu Islands; Korea (TAKAKUWA, 1941; PAIK, 1976; LIM, 1988; GOLOVATCH, 1980).
- 16.2. **Anaulaciulus koreanus tuberculatus** (Takakuwa, 1941)
Fusiulus koreanus tuberculatus: TAKAKUWA, 1941 (FIG. 19)
Anaulaciulus koreanus tuberculatus: ENGHOFF, 1986 Korea: Hoko (PAIK, 1976; LIM, 1988).
17. **Anaulaciulus kuritai** (Murakami, 1966)
Fusiulus kuritai: MURAKAMI, 1966 (FIG. 1)
Anaulaciulus kuritai: ENGHOFF, 1986 Japan: Shikoku.
18. **Anaulaciulus longus** (Takakuwa, 1941)
Fusiulus longus: TAKAKUWA, 1941 (FIGS 6-7)
Anaulaciulus longus: ENGHOFF, 1986 Japan: Akiyoshi; Korea (LIM, 1988).
- *19. **Anaulaciulus nepalensis** Korsós, in press
Anaulaciulus nepalensis: KORSÓS, in press (FIGS 1, 3, 7, 10, 48-52) Nepal.

20. **Anaulaciulus niger** Korsós, in press
Anaulaciulus niger: KORSÓS, in press (FIGS 53-58) Nepal.
21. **Anaulaciulus okinawaensis** Shinohara, 1990
Anaulaciulus okinawaensis: SHINOHARA, 1990 (FIG. 1) Japan: Ryukyu Islands.
22. **Anaulaciulus onychophora** (Takakuwa, 1942)
Fusiulus onychophora: TAKAKUWA, 1942 (FIGS 1-2)
Anaulaciulus onychophora: ENGHOFF, 1986 Japan: Honshu.
23. **Anaulaciulus otigonopus** Zhang, 1993
Anaulaciulus otigonopus: ZHANG, 1993 (FIGS 1-7)
Anaulaciulus otigonopus: KORSÓS, 1994
Anaulaciulus otigonopus: KORSÓS, in press China: Hunan Province, Changsa.
24. **Anaulaciulus pakistanus** Korsós, in press
Anaulaciulus pakistanus: KORSÓS, in press (FIGS 59-60) Pakistan: Swat.
25. **Anaulaciulus paludicola** Pocock, 1895
Anaulaciulus paludicola: POCK, 1895
Anaulaciulus paludicola: CAUSEY, 1966 (FIGS 1-6) China: Wo-Lee Lake.
26. **Anaulaciulus pinetorum** (Attems, 1909)
Fusiulus pinetorum: ATTEMS, 1909 (FIGS 14-16, 69-75)
Fusiulus pinetorum: SHINOHARA, 1960 (FIG. 18)
Anaulaciulus pinetorum: ENGHOFF, 1986 Japan: Honshu.
- 26.1 **Anaulaciulus pinetorum nivalis** (Verhoeff, 1941)
Fusiulus pinetorum nivalis: VERHOEFF, 1941b (FIGS 8-10)
Fusiulus ciliatus: Shinohara, 1960 (FIGS 14-17): ENGHOFF, 1986
Anaulaciulus pinetorum nivalis: ENGHOFF, 1986 Japan: Honshu.
27. **Anaulaciulus quadratus** (Takakuwa, 1941)
Fusiulus quadratus: TAKAKUWA, 1941 (FIGS 14-16)
Anaulaciulus quadratus: TAKANO, 1978
Anaulaciulus quadratus: ENGHOFF, 1986 Japan: Honshu.
28. **Anaulaciulus riedeli** Jedryczkowski, 1982
Anaulaciulus riedeli: JEDRYCZKOWSKI, 1982 (FIGS 19-27)
Anaulaciulus riedeli: ENGHOFF, 1986 Korea: Hyangsan, Kyongsong and Puryong districts.
29. **Anaulaciulus ryugadensis** Shinohara, 1990
Anaulaciulus ryugadensis: SHINOHARA, 1990 (FIG. 2) Japan: Shikoku.
30. **Anaulaciulus simodanus** (Takakuwa, 1941)
Fusiulus simodanus: TAKAKUWA, 1941 (FIGS 8-9)
Anaulaciulus simodanus: ENGHOFF, 1986 Japan: Honshu.
31. **Anaulaciulus simplex** Verhoeff, 1936
Fusiulus simplex: VERHOEFF, 1936
Anaulaciulus simplex: SHINOHARA, 1973
Anaulaciulus simplex: ENGHOFF, 1986 Japan: Honshu, in caves widely distributed (SHINOHARA, 1973); Taiwan (WANG, 1963; SHINOHARA, 1973).
32. **Anaulaciulus takakuwai** (Verhoeff, 1941)
Fusiulus takakuwai: VERHOEFF, 1941a (FIGS 37-38)
Anaulaciulus takakuwai: ENGHOFF, 1986
subspecies:
Anaulaciulus takakuwai coloratus (Verhoeff, 1941)
Fusiulus takakuwai coloratus: VERHOEFF, 1941a (FIG. 39)
Anaulaciulus takakuwai coloratus: ENGHOFF 1986 Japan: Honshu.
33. **Anaulaciulus takanoi** Shinohara, 1990
Anaulaciulus takanoi: SHINOHARA, 1990 (FIG. 3) Japan: Honshu.
34. **Anaulaciulus tibetanus** Korsós, in press
Anaulaciulus tibetanus: KORSÓS, in press (FIGS 61-63) China: Tibet; India: Assam.
35. **Anaulaciulus tigris** Korsós, in press
Anaulaciulus tigris: KORSÓS, in press (FIGS 5, 12, 64-69) Pakistan: Swat.
36. **Anaulaciulus tongosanensis** Paik, 1976
Fusiulus longus Takakuwa, 1941: sensu PAIK, 1963
Fusiulus tongosanensis: PAIK, 1976 (FIGS 1-11) Korea: Mt. Tonggo-san (LIM, 1988).

37. **Anaulaciulus tonginus** (Karsch, 1881)
Iulus tonginus: KARSCH, 1881
Anaulaciulus tonginus: ENGHOFF, 1986
Anaulaciulus tonginus: KORSÓS, 1994 (FIGS 1-8)
Fusiulus trilobus khuuae Wang, 1963: KORSÓS, 1994
 Hong Kong; Taiwan.
38. **Anaulaciulus topali** Korsós, in press
Anaulaciulus topali: KORSÓS, in press (FIGS 70-75)
 India: Jammu and Kashmir.
39. **Anaulaciulus trapezoidus** (Wang, 1955)
Fusiulus trapezoidus: WANG, 1955 (FIG. 3)
Anaulaciulus trapezoidus: ENGHOFF, 1986
 Taiwan.
40. **Anaulaciulus trigonalis** (Takakuwa, 1941)
Fusiulus trigonalis: TAKAKUWA, 1941 (FIGS 4-5)
Anaulaciulus trigonalis: ENGHOFF, 1986
 Japan: Kyushu, Kagoshima.
41. **Anaulaciulus trilobus** (Wang, 1963)
Fusiulus trilobus quemoyensis: WANG, 1963
Anaulaciulus trilobus: ENGHOFF, 1986
 Taiwan: Quemoy Island.
42. **Anaulaciulus vallicola** (Pocock, 1895)
Iulus vallicola: POCKOCK, 1895 (FIG. 13)
Anaulaciulus vallicola: CAUSEY, 1966 (FIG. 7)
 China: Che Kiang, Da-Zeh valley.
43. **Anaulaciulus yamashinai** (Verhoeff, 1939)
Fusiulus yamashinai: VERHOEFF, 1939b (FIGS 1-3)
Fusiulus jamashinai Verhoeff, 1941a (FIGS 40-42): ENGHOFF, 1986
Fusiulus insularumi Verhoeff, 1941a: ENGHOFF, 1986
Fusiulus yamashinai: TAKAKUWA, 1941 (FIG. 1)
Anaulaciulus yamashinai: ENGHOFF, 1986
 Japan: Ryukyu Islands.
44. **Anaulaciulus yosidanus** (Takakuwa, 1941)
Fusiulus yosidanus: TAKAKUWA, 1941 (FIGS 20-21)
Anaulaciulus yosidanus: ENGHOFF, 1986
 Japan: Honshu.

INTRAGENERIC RELATIONSHIPS

The only internal classification of the genus appears in the division by VERHOEFF (1941b) where he, on the occasion of a new subspecies, *Fusiulus pinetorum nivalis*, erected the subgenus *Parfusiulus* for all the other members of the genus. The only species, *pinetorum* (with the subspecies *nivalis*) remained in the subgenus *Fusiulus* s. str. in his sense. However, the distinguishing character (i.e. two hairy fields on the mesal and lateral lamellae of the opisthomerites) seems not to be warranted, especially in the light of a more careful study of the gonopodal details in other species. As a result, virtually all species of the genus have more-or-less hairs on their opisthomerit lamellae.

According to an examination of the shape of the telopodites of the posterior gonopods, the following preliminary species-groups in the genus can be presented.

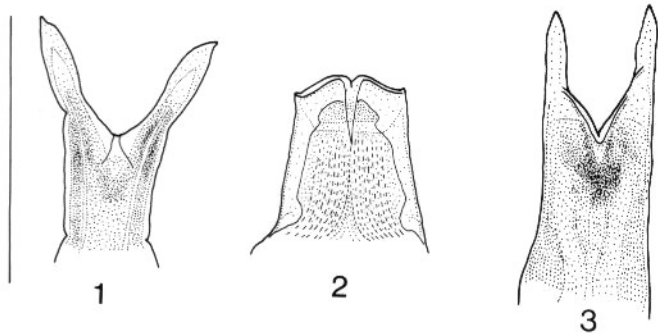
1. *yamashinai*-group (cf. Figs 8-11): *acutus*, *bilobus*, *cornutus*, *komatsui*, *onychophora*, *pinetorum*, *quadratus*, *trigonalis* and *yamashinai*
2. *paludicola*-group (cf. Figs 5-6): *koreacolus*, *longus*, *paludicola*, *riedeli*, *simodanus* and *tonggosanensis*
3. *koreanus*-group: *koreanus*, *okinawaensis*, *trapezoidus*
4. *hirosaminus*-group: *hirosaminus*, *kuritai*
5. *simplex*-group (cf. Fig. 7): *attemsii*, *simplex*
6. *tonginus*-group: *otigonopus*, *tonginus*, *trilobus*
7. *inaequipes*-group: *acaudatus*, *bilineatus*, *enghoffi*, *inaequipes*, *kashmirensis*, *nepalensis*, *niger*, *pakistanus*, *tibetanus*, *tigris* and *topali*

The species *takakuwai* can be considered as a bridge-species between the *paludicola*-group and the *koreanus*-group (based purely on gonopod comparison).

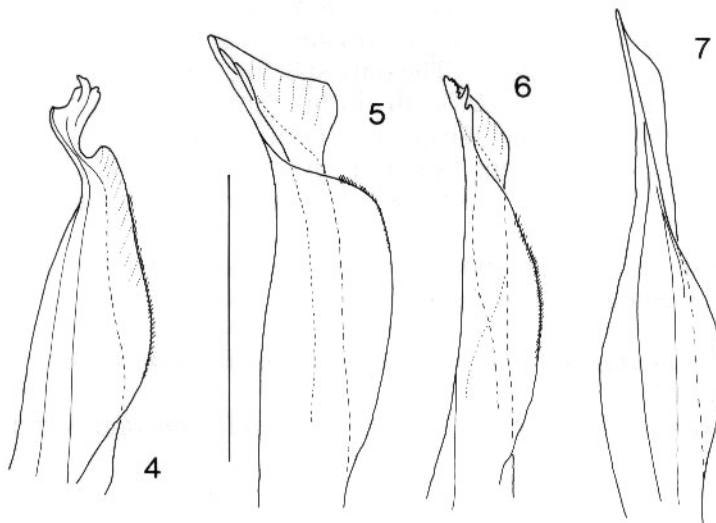
Six species could not be inserted in the groups above: *capillatus*, *golovatchi* (Fig. 4), *kiusiensis*, *ryugadensis*, *takanoi*, *yosidanus*. In some cases their gonopods are so peculiar (e.g., in *takanoi*) that even their validity within the genus *Anaulaciulus* may be question-marked. (The original description of this species does not deal with some important features like penis structure, etc.).

One species, *vallicola* is known only by female, and although the type specimen has been redescribed by CAUSEY (1966) and also seen by the author, nothing can be said about its position in the genus.

Based on some fresh material, kindly loaned by Dr. H. ONO (National Science Museum, Tokyo) some preliminary sketches are given to illustrate two main general pattern series. Figures 5 to 7 (samples from Korea and Japan) show the line of complete reduction of the opisthomerites, from a "paludicola"-type gonopod to a simple "needle". *Anaulaciulus golovatchi* (Fig. 4, drawn from a paratype kindly loaned by Dr. S. I. GOLOVATCH, Moscow) may perhaps also be inserted in this series.



FIGS 1-3. — Penis, caudal view. - 1: *Anaulaciulus bilineatus* Korsós, in press from Nepal. - 2: *Megaphyllum unilineatum* (C. L. Koch, 1838) from Beograd, Yugoslavia. - 3: *Anaulaciulus koreanus* (Verhoeff, 1939) from North Korea. Scale 0.5 mm.

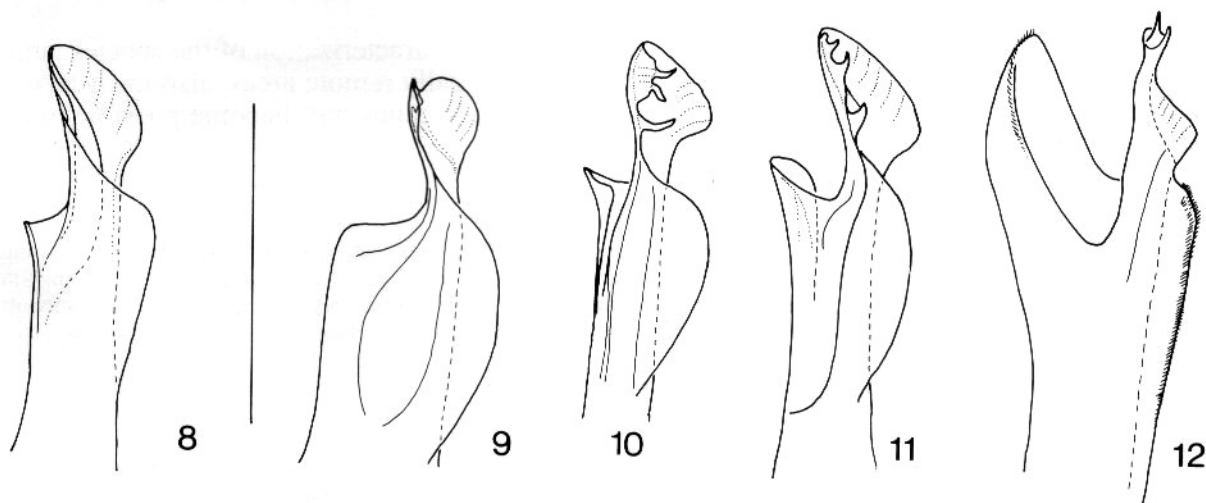


FIGS 4-7. — Left opisthomerit, frontal view. - 4: *Anaulaciulus golovatchi* Mikhajlova, 1982, paratype. - 5: Specimen from North Korea, Mt. Paekdu-san. - 6: Specimen from Japan, Ryukyu Islands, Tokara. - 7: Specimen from Japan, Ryukyu Islands, Amami. Scale 0.5 mm.

The other line is more complicated but some characteristics can be observed. The lateral lamellae of the opisthomerit appears as a "shoulder" (Fig. 8) and later, through a series of intermediates (Figs 9-11), develops into a broad "wing" (Fig. 12) as it is seen in the *inaequipes*-group. Although all this drawings are based on species originated from Japan, there is a striking resemblance between the gonopods of the specimen from Honshu (Gifu) and those of the

members of the *inaequipes*-group (cf. KORSÓS, in press). However, the lack of a proper "beak" surely allocates it in another relationship. The samples investigated for this study are certainly including several new forms, which will be dealt in future investigations.

It was already pointed out elsewhere (KORSÓS, 1994), that *Anaulaciulus tonginus* (and the similar - maybe synonymous - species, *otigonopus* and *trilobus*) is believed to have a somewhat peculiar position in the genus. Not only its intermediate penis and gonopod structure (thick, antero-posteriorly not so flattened promerites; peculiar telopodits with a beginning of a "beak" yet densely haired), but also its central geographical distribution (Hong-Kong, Taiwan, and maybe other parts of southeastern China) implies that it is close to the theoretical ancestor of the whole genus.



FIGS 8-12. — Left opisthomerite, frontal view. - 8: Specimen from Japan, Honshu, Chojaga mori. - 9: Specimen from Japan, Kyushu, Nagasaki. - 10: Specimen from Japan, Kyushu, Yaku-shima. - 11: Specimen from Japan, Kyushu, Kumamotol. - 12: Specimen from Japan, Honshu, Gifu. Scale 0.5 mm.

CONCLUSIONS

It is clear from the present observations, that the shape of the scale-like promerite is very variable in the populations and that it is not a reliable character for distinguishing species. This was already introduced by MIKHAJLOVA (1982), and further discussed by KORSÓS (in press). Unfortunately, descriptions of former species, in some cases, have been exclusively based on the shape of the promerite (e.g., *acutus*, *bilobus* & *quadratus*, all by TAKAKUWA, 1941). The degree of the morphological variability of the opisthomerites is still to be defined, and a clarification may well be resulted in a number of synonymies in the species-groups outlined above.

Female (vulval) characters, as often neglected before, are also in urgent need to redescribe. The species in the *inaequipes*-group (KORSÓS, in press) show relatively consistent pattern in the internal structure of bursa, usually having a simple or slightly curved apodemetic tube and a more-or-less sphaerical ampulla; whereas other species may have more complicated apodemetic tube (*golovatchi*), or an ampulla strongly elongated (*tonginus*, *riedeli*, *kiusiensis*) or with a distinct appendix (*koreanus*).

As it was shown by the analysis of the *inaequipes*-group, external characters have usually an emphasized importance in distinguishing the different species. General body colouration

(longitudinal stripes e.g., in *bilineatus*, bright yellow ground colour with dark brown blotches ordered according to pro- and metazona: as in *tigris* and *pakistanus*) is more characteristic to several species than the gonopod conformation, and may also be more useful in separating them. Outside the *inaequipes*-group, one can also find similar feature: *golovatchi*, *paludicola*, *tonginus* and *yamashinai* show three black, longitudinal stripes.

The shape of the epiproct may also help in distinguishing the species, while members of the *inaequipes*-group never have a preanal project turned upwards (usually it is short, straight, or missing), the same character state, to a different degree, is not rare in the other continental and in the Japanese species (e.g., in *golovatchi*, *koreacolus*, *riedeli*, *ryugadensis*, *takanoi* & *tonginus*).

In some cases, maybe due to coexistence, significant size differences appear in closely related species-pairs (*nepalensis-niger*, *pakistanus-tigris*). This phenomenon is analyzed in more detail elsewhere (KORSÓS, in press).

Future investigations should aim at the more accurate characterization of the species, and, with the accumulation of large material from the geographically remote areas, also from Japan, the internal relationships of this highly diverse and complex genus will become possible to be clarified.

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