OBSERVATIONS ON THE SPERMATOGENESIS OF SOME SCARABAEOID BEETLES[1]

During July and August 1965, the writer spent a month at the Department of Entomology, Oregon State University, Corvallis, Oreg., working on the spermatogenesis of various scarabs and two lucanids. These were reared or collected by Dr. P. O. Ritcher, Head of the Department, and Research Assistants Charles Baker, James Cornell, and David Mays. The results are shown in table 1.

Adults of *Trox foveicollis* Harold, *Trox spinulosus dentibius* Robinson, and *Trox punctatus* Germar, sent by Charles Baker from Corvallis, were studied by Miss Caridad Purcell and me in Puerto Rico.[2] It was found that the two former species, belonging to the *scaber* group of *Trox*, have metacentric autosomes, whereas *Trox punctatus*, a species from the *suberosus* group, has acrocentric autosomes.

The findings on *Trox foveicollis* were confirmed in Corvallis. *Trox scaber*, another species from the *scaber* group, also had all autosomes metacentric, and two other species of the *suberosus* group, *Trox monachus* and *Trox scutellaris*, had all autosomes acrocentric. This is a very interesting finding. Since there is no difference in chromosome number between *scaber* and *suberosus* group, the shift of the centromere location must be due to pericentric inversions in the autosomes.

Metacentry is typical of Scarabaeidae. Therefore, the *suberosus*-type karyotype must be the new one. It is most unlikely that such a karyotype rearrangement could happen suddenly. Most probably the *suberosus* group has a long evolutionary history separated from other groups of *Trox*. There has apparently been a phase in the history of *suberosus* where the pericentric inversions were of great adaptive value and became established. Also, those early species must have had a special readiness for this type of rearrangement. Thus a series of successive rearrangements of similar type, pericentric inversions, followed, according to the principle called karyotypic orthoselection by M. J. D. White.[3] This is the first record in Coleoptera of a complete inversion series. It would be very interesting to study more *Trox* species, especially of other continents, although it may be no longer possible to find intermediate species between *scaber* and *suberosus*.

The spermatogenesis of all *Trox* species studied starts very late, meiotic divisions appearing in adults 7 weeks old or older. The duration of the spermatogenetic period is probably quite long.

[1] This work was supported by NSF Grant GB-3586 (Ritcher).

[2] Purcell, Caridad M., and Virkki, Niilo, Two *Trox* karyotypes differing radically in the location of centromere, *J. A. Univ. P. R. 50:* 158-60.

[3] White, M. J. D., Principles of karyotype evolution in animals, *Genetics Today, Proc.* XI Intern. Congr. Genetics, pp. 391-7, 1964.

TABLE 1.—*Results of an investigation of spermatogenesis of some scarab beetles in Oregon, July and August 1965*

Species	Karyotype	Initiation and course of spermatogenesis	Remarks
1. *Trox foveicollis* Harold	$9 + Xy_p$	Adults from 7th week on	All autosomes metacentric
2. *Trox spinulosus dentibius* Robinson	$9 + Xy_p$	do.	Do.
3. *Trox scaber* (L.)	$9 + Xy_p$	do.	Do.
4. *Trox punctatus* Germar	$9 + Xy_p$	do.	All autosomes acrocentric
5. *Trox monachus* Herbst	$9 + Xy_p$	do.	Do.
6. *Trox scutellaris* Say	$9 + Xy_p$	do.	Do.
7. *Glaresis* sp.	$9 + Xy_p$	Adults	
8. *Lichnanthe rathvoni* Lec.		Prepupa and first week of pupa	
9. *Sinodendron rugosum* Mann.	$8 + Xy_p$	During pupal stage	
10. *Ceruchus strictus* Lec.		Late pupa and adult	
11. *Pleocoma crinita* Linsley	$9 + Xy_p$	Pupal stage; metaphases from 20th pupal day on	Frequency of ring bivalents unusually high for a scarab
12. *Pleocoma dubitalis* Davis	$9 + Xy_p$	do.	Do.
13. *Pleocoma minor* Linsley	$9 + Xy_p$	do.	Do.
14. *Pleocoma simi* Leach	$9 + Xy_p$	do.	Do.
15. *Serica falli* Dawson	$9 + Xy_p$	Pupa and young adult	
16. *Diplotaxis sierrae* Fall	$9 + Xy_p$	do.	
17. *Diplotaxis obscura* Lec.	$9 + Xy_p$	do.	
18. *Polyphylla decemlineata* (Say)		Pupa	
19. *Ligyrodes relictus* (Say)	$9 + Xy_p$	Adults	
20. *Cremastocheilus armatus* Walker	$9 + Xy_p$	Adults from 3d week on	
21. *Psammodius oregonensis* Cartwright	$9 + Xy_p$	Adults	
22. *Aegialia blanchardi* Horn	$9 + Xy_p$	Adults	Conspicuous secondary growth of spermatocytes

The *Trox*-related *Glaresis* has metacentric chromosomes. The Y chromosome is very tiny. Spermatogenesis was observed in adults of unknown age, and all of them had all meiotic stages, although some specimens had their testes nearly empty. The initiation of spermatogenesis may be earlier, with a duration similar to that of *Trox*.

Lichnanthe rathvoni has the earliest initiation of spermatogenesis known to occur in beetles. Spermatogenesis was over and no gonia remained in 9-day-old pupae. The process probably starts in the prepupa; if it starts in early pupae, it must proceed in one big wave.

The lucanid *Sinodendron rugosum* also has an early start of spermatogenesis in 1-day-old pupae, but the process continues during the whole pupal life. Only very young adults show remnants of it. Similarly, no meiosis was ever encountered in adult males of the Finnish *Sinodendron cylindricum* L. No clue was found of how *S. rugosum* has lost one pair of autosomes. It could be by neo-XY formation, however, because karyotypes 9 + X and 8 + neo-XY occur in Lucanidae.

The spermatogenesis starts much later in the other lucanid, *Ceruchus strictus*. A white pupa with dark eyes, a more darkened pupa, and a young adult had practically the same testis picture: abundant prophase until late diplotene, but no later stages. The karyotype could not be determined.

The four species of *Pleocoma* studied have quite uniform chromosome relationships. The autosomes are quite large, metacentric, and two to four of them tend to associate with the sex bivalent, apparently by means of nucleolus material. *P. crinita* has approximately two rod-shaped autosome bivalents, whereas *P. minor* has only ring bivalents. The significance of such minor differences is hard to evaluate, because chiasma frequency depends also on factors of milieu.

The initiation and course of spermatogenesis was studied in more detail in *Pleocoma crinita*. For it, a series of 13 male pupae of known age was available. From earlier attempts made during the past several years, with material mailed from Oregon to Puerto Rico by Dr. Ritcher, it was clear that young male pupae and adults do not show meiotic divisions. Young pupae have spermatogonia and meiotic prophases, the first meiotic divisions occurring more or less simultaneously with the initiation of eye pigmentation, around the 20th day of pupal life. Pupae with grey eyes are good for studying all phases of spermatogenesis. There is individual variation in the initiation and course of divisions; apparently this variation is related to variation in duration of the pupal stage (from 39 to 53 days at 15°C., according to Ellertson and Ritcher).[4] Pupae with eyes just turned dark

[4] Ellertson, F. E., and Ritcher, P. O., Biology of Rain Beetles, *Pleocoma* spp., Associated with Fruit Trees in Wasco and Hood River Counties, Oreg. Agr. Exp. Sta. Tech. Bull. 44:1-42, 1959.

grey were found to be at the height of meiotic activity in other *Pleocoma* species also. At the end of the pupal period, spermatogenesis is over in *Pleocoma*, with no germarium left.

Serica falli and two species of *Diplotaxis* exhibited the same type of spermatogenesis found in other melolonthine scarabs: small and very numerous spermatocytes, considerably later initiation of spermatogenesis (in last half of pupal life), and a karyotype of $9 + Xy_p$.

In *Serica*, spermatogenesis starts somewhat earlier, or proceeds more rapidly, because spermatozoa form the main contents of the adult testes. The Finnish *Serica brunnea* L., studied earlier, never had meiotic divisions in adults. This observation runs parallel with another. The Finnish *Melolontha hippocastani* Fabr. has no more meiosis in the adult male,[5] whereas the Central European *M. melolontha* L. has it.[6] Rapid spermatogenesis may be an adaptation to the short breeding period in the North.

In *Polyphylla decemlineata* meiosis was completely over in field-collected adult males. One male of the dynastid *Ligyrodes relictus* was studied on the day of its emergence as an adult. Spermatogenesis had started in the pupa, and a few spermatocysts had proceeded until the meiotic metaphases. No spermiohistogenesis or spermatozoa were present. Spermatogenesis probably is long-lasting, as is usual in dynastines.

Cremastocheilus armatus is a cetonine beetle with comparatively late initiation of spermatogenesis. Meiotic prophases were encountered in recently emerged and young adults up to the third week of adult life. Older specimens were not available at the time the study was made.

Adult males of unknown age of *Psammodius oregonensis* and *Aegialia blanchardi* were dug from dunes at the Oregon coast. Both had meiosis in full force. Although the karyotypes look similar in both species, the extrachromosomal cytology is quite different. *Psammodius* has more trivial cell relationships, whereas *Aegialia* shows a conspicuous diplotenic growth of the spermatocyte, and, accordingly, very long spermatozoa. These characteristics of *Aegialia blanchardi* suggest a close relationship with *Aphodius* and *Onthophagus*, and especially to *Aphodius*.

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[5] Virkki, Niilo, Zur Zytologie einiger Scarabaeiden, *Ann. Zool. Soc. "Vanamo" 14:* 1–104, 1951.

[6] Landa, V., Development and function of imaginal male reproductive organs of the cockchafer *Melolontha melolontha* L., pp. 111–4, in: Hrdý, I. (ed.), The Ontogeny of Insects, Czechoslovak Academy of Sciences, Prague, 406 pp., 1959.