

General Discussion

In many animals, the first clue of the parthenogenesis has been provided by the absence of males in natural populations. Further studies are needed for making the parthenogenesis more reliable, such as on the biased sex ratio of neonates (Hamilton, 1953, 1955; Cole, 1975; Harker, 1997), on the production of the successive generations without male participation (Hamilton, 1953, 1955; Cole, 1975; Harker, 1997), and on the processes and mechanisms of egg maturation and parthenogenetic start of embryogenesis (see review by Cuellar, 1987).

In some parthenogenetic animals, the maturation division is inhibited to produce diploid eggs directly developing into embryos (ameiotic or apomictic parthenogenesis) (in some weevils, Suomalainen, 1969; Takenouchi, 1969; Lokki *et al.*, 1976, two tardigrades, Rebecchi and Bertolani, 1988, and root-knot nematodes, Van Der Beek *et al.*, 1998). In the other, the maturation division is normal to produce haploid eggs, in which the diploidy has to be recovered before the embryonic development (meiotic or automictic parthenogenesis). In the meiotic parthenogenesis, various modes have been known for the recovery of diploidy, such as the fusion between the egg nucleus and the sister second polar body nucleus both derived from the secondary oocyte nucleus (in a sawfly *Pristiphora*

pallipes, Comrie, 1938, and a root-knot nematode *Meloidogyne halpa* race A, Van Der Beek *et al.*, 1998), the fusion of the egg nucleus with one of the non-sister second polar nuclei derived from the first polar body nucleus (in a dipteran *Lonchoptera dubia*, Stalker, 1956, a brine shrimp *Artemia salina*, Stefani, 1960, and a stick insect *Bacillus whitei*, Marescalchi *et al.*, 1991), the reunite of two haploid chromosome sets at the anaphase of the second maturation division (in a brine shrimp *A. salina*, Barigozzi, 1944), the fusion between the secondary oocyte nucleus and the first polar body nucleus (in a stick insect *B. atticus atticus*, Marescalchi *et al.*, 1993), the abortive first maturation division (in a moth *Solenobia* sp., Narbel-Hofstetter, 1950), halving of chromosomes having been doubled into $4n$ prior to meiosis (in some lumbricid earthworms, Muldal, 1952, and a whiptail lizard *Cnemidophorus uniparens*, Cuellar, 1971), halving of those having been doubled into $4n$ by the end of the meiotic prophase (in some stick insects, Pijnacker, 1966; Koch *et al.*, 1972; Pijnacker and Ferwerda, 1978; Marescalchi *et al.*, 1991), by fusion of two haploid blastomere nuclei during embryogenesis (in a locust *Locusta migratoria*, Pardo *et al.*, 1995), and the doubling of chromosomes in embryonic cells by C-mitosis and endomitosis (in a stick insect *B. rossius*, Pijnacker, 1969). All of these results are of very exciting, but most of them were described based upon only a few specimens and some of them lacked the confirmation of virgin birth. Some of these results, therefore, may need

to be strengthened by reexaminations.

In the scorpions, there have been no study on the processes and mechanisms of the parthenogenesis. In the present study, I have long continued examinations on the parthenogenesis in the viviparous scorpion, *Liocheles australasiae*. Virgin birth has been confirmed based on some different examinations, such as separate rearing through generations and histological surveys through the reproductive systems. In Part 1 of the present study, I have obtained a number of specimens enough for the three different methods to make the process and mechanism of parthenogenesis certain in Part 2.

In Part 2 of the present study, the process and mechanism of egg maturation and parthenogenetic start of embryogenesis have been described in detail in *Liocheles australasiae* through the histological, karyological, and DNA quantificational methods. Eggs matured through the ordinary two maturation divisions. The diploidy was recovered by a fusion between the egg nucleus and the second polar body nucleus both derived from the secondary oocyte nucleus and then the diploid single-cell embryo started embryogenesis. A first polar body or two second polar bodies derived from the first polar body remained adjacent to each early embryo, suggesting that the first polar body and its descendants cannot participate in the recovery of diploidy. The process and mechanism of egg maturation and recovery of diploidy were supported and strengthened by

the results of karyological and DNA quantificational studies.

In the present thesis, I have obtained two new results on the thelytokous parthenogenesis in *Liocheles australasiae*, the parthenogenetic reproduction through four generations and the parthenogenetic recovery of diploidy by fusing between the egg nucleus and the second polar body nucleus. The latter result is similar to those in a brine shrimp (Artom, 1931), a sawfly (Comrie, 1938), and a coccid (Suomalainen, 1950), but it is based on much more laborious works and some new bases of evidence.