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Reproductive success of large and small flies in *Drosophila bipectinata* complex

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Reproductive success of large and small flies of *Drosophila malerkotliana* and *D. bipectinata* has been studied using no-choice method. Results indicate that large males have higher remating ability and longevity than small males as a result of which they can inseminate more females in their lifetime than small males. Large females also have higher reproductive success because they have more number of overioles, lay more eggs and produce more fertile offspring than the small female and also mate with more males in their lifetime than small female by having higher longevity. These findings suggest that large flies have higher reproductive success than small flies.

BODY size is the most obvious, easily observable and measurable phenotypic trait and there is compelling evidence indicating that it is directly related to fitness[1]. In *Drosophila*, as in many organisms, body size is closely linked to life history traits such as fecundity, dispersal ability and mating success[2–4] and has been widely used in studies on quantitative genetics[5]. The adaptive nature of body size in *Drosophila* has also been demonstrated by many workers both in natural populations[6,7] and in laboratory populations[8,9]. Body size also influences mating speed, fecundity and other fitness characters[10–13].

Many workers have used thorax length as an index of body size in *Drosophila*[12–14]. Apart from thorax length, other morphological traits such as wing length, wing width and face width have been used as index of body size. Wing is another phenotypic trait which can be used as an index of body size[15,16]. Relationship between wing length and mating speed had been studied in *D. malerkotliana*[16]. Correlation between copulation duration and fertility; and variation in mating propensity had also been studied in *D. bipectinata*[17–19]. The fitness characters such as fecundity, fertility, male remating ability and longevity of large and small flies have not been made. Moreover, mating speed alone does not qualify an individual to have higher reproductive success. Hence the present investigation is aimed at understanding reproductive success of large and small flies in *D. bipectinata* species complex.

The stocks used in the present study were *Drosophila malerkotliana* and *D. bipectinata*. All experiments were made separately for each of these two species. The stocks used in the present study originated from 150 naturally inseminated females from Mysore, Karnataka. When progeny appeared, flies were distributed to different culture bottles and were maintained under constant temperature (22 ± 1°C). For every generation, flies multiplied in different culture bottles were mixed together and eggs were collected using Delcour's[20] procedure. Eggs (100) were seeded in fresh quarter pint milk bottles with 25 ml of wheat cream–agar medium to avoid larval competition during development (this procedure allows us to reduce environmental variation in size). After 10 generations, when adults emerged, virgin females and males were isolated within 3 h of their eclosion and maintained separately at 22 ± 1°C. Wing lengths of male and female flies were measured separately when they reached the required age. Each fly was etherized individually, the intact left wing kept in horizontal plane was measured from humeral cross vein to the tip with an ocular micrometer at 100 × magnification. Wing length was measured in units of 1/10 mm. After measuring the wing length, each fly was placed separately in fresh food vials to study fitness characters.

To study fecundity and fertility, five to six-day-old virgin females and bachelor males of chosen wing size (see Table 1 for chosen wing size) were taken and different crosses were made (large male × large female; large male × small female; small male × large female; small male × small female). Soon after mating, mated females were transferred into fresh food vials every 24 h without etherization. The total number of eggs laid in each vial and the total number of progeny appeared were counted over a period of 15 days. 50 trials were run for each cross and mean fecundity and fertility were obtained.

To study the remating ability of male, 5 to 6-day-old virgin females and bachelor males of chosen wing size (see Table 1 for chosen wings size) were taken and different crosses were made (large male × large female; large male × small female; small male × large female; small male × small female). When mating occurred, the pair was allowed to complete copulation. After

Table 1. Fitness characters of different crosses

Parameters	Large male × Large female	Large male × Small female	Small male × Large female	Small male × Small female	*F*-value
A: *Drosophila malerkotliana*	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	
Fecundity	313.24 ± 4.01	281.35 ± 6.07	309.27 ± 5.57	268.09 ± 0.58	15.84*
Fertility	305.71 ± 3.87	268.86 ± 5.02	303.00 ± 5.04	233.86 ± 5.55	43.27**
Remating ability of male	5.66 ± 0.14	5.56 ± 0.13	3.00 ± 0.08	3.46 ± 0.14	28.47**
B: *Drosophila bipectinata*					
Fecundity	262.39 ± 2.91	215.40 ± 2.36	249.38 ± 3.09	199.34 ± 1.81	133.17**
Fertility	249.79 ± 2.54	204.00 ± 2.87	236.11 ± 2.94	186.84 ± 2.13	125.56**
Remating ability of male	4.84 ± 0.17	5.52 ± 0.25	3.20 ± 0.18	3.64 ± 0.21	16.05*

Mean values are reported with standard error *$P < 0.05$; ** $P < 0.01$.

	D. malerkotliana	*D. bipectinata*
Large male	(17.06 units)	(17.28 units)
Small male	(14.34 units)	(14.04 units)
Large female	(18.39 units)	(19.36 units)
Small female	(15.88 units)	(16.32 units)

Wing length of large and small flies is given in parenthesis.

copulation, the mated female was aspirated out and replaced with another virgin female and the same procedure repeated. Observation was made for 2 h and the number of females mated by single male was recorded. If there was no mating within 2 h, then the pairs were discarded. The remating ability of 50 males (trials) were studied for each cross and mean remating ability of male was calculated.

One-way analysis of variance was carried out on mean values of fecundity, fertility and remating ability of male.

Five to six days old large and small females of chosen wing length (see Table 1 for chosen wings size) were used to determine the number of ovarioles in them. Individual females were separately dissected out in a drop of physiological saline under binocular stereomicroscope. The ovarioles of each ovary were separated from each other with a fine needle and counted. Student's *t* test was carried out on mean number of ovarioles/individual of 25 large and 25 small individuals.

To measure longevity, virgin females and bachelor males of chosen wings size (see Table 1 for chosen wings size) were taken and different crosses were made as above. One female and a male were transferred into fresh food vials containing wheat cream–agar medium. Active yeast was also added to vials 48 h prior to use. Vials were renewed daily during measurement of longevity. All cultures were maintained at 22 ± 1°C and at a 12:12 light/dark cycle. Adult longevity is measured here from the date of completed eclosion to the death of an individual. A total of 50 replicates was made for each cross.

Sexual selection is common among animals because the female's reproductive success is limited by the number of eggs she can produce in her lifetime and a male's reproductive success is limited by the number of females he can inseminate. In the present study, data on fecundity and fertility (Table 1) show the advantage of large size in both *D. malerkotliana* and *D. bipectinata*. Both fecundity and fertility were highest in crosses involving males and females with long wings and lowest in crosses involving females with short wings. This is in conformity with the work of Singh and Mathew[21,22] who, while working in *D. ananassae*, reported that flies possessing high number of sternopleural bristles are larger in size than those with low number of bristles. The flies with high number of bristles show greater mating success and produce more progeny than those with low number of bristles.

Table 1 also shows the data on remating ability of male in different crosses. According to these data, the remating ability of large male crossed with large female was more when compared to small male crossed with small female, indicating that a large male can inseminate more females and produce more fertile offsprings than a small male. The data presented in Table 1 also show that males of both *D. malerkotliana* and *D. bipectinata* have remating ability. In *Drosophila*, males of many species have this ability[23–25]. Table 1 also show that a large male has higher remating ability than small males. The remating ability was highest when the large male was allowed to mate with large female. With higher remating ability and aggressiveness, the large male can inseminate more females in a multiple-choice situation or in nature and increase its fitness than small males. Even in *D. bipectinata*, though the remating ability was slightly different from that of *D. malerkotliana*, the larger male had higher remating ability.

The size of the ejaculate is also an important factor which determines the fitness of males. No direct evidence could be obtained on the size of the ejaculate or the number of sperms that enter the female genital tract. In *Drosophila* when copulation occurs, the sperms are stored in the spermatheca and fertilized eggs are released. The female is able to receive the second male only when most of the sperm in the spermatheca are exhausted. Thus the female remating interval provides some evidence on the size of the ejaculate. Our unpublished data on remating interval show that when a large female is mated by a small male, the remating interval is short (in terms of days) because it receives lesser number of sperms and it has to receive the males more frequently than the large male. When a small female is mated by a large male, the remating interval is long and confirms that a large male has an advantage over small males. According to Gruwez *et al.*,[26] higher fecundity of female is correlated with number of ovarioles present in it. The present data on wing length and number of ovarioles (Figure 1) show that large females have more number of ovarioles than small ones. These observations agree with the findings of Montague[27] who demonstrated that larger females carry more ovarioles and have higher potential fecundity and Santos *et al.*[13] who found positive correlation between thorax length and number of ovarioles in *D. buzzatii*.

Large males are capable of inseminating more females than small males[11] and transfer more sperm per ejaculate. Large females with more number of ovarioles when mated by a large male therefore can receive and store more sperms than small females and this offers greater fitness advantage for large individuals.

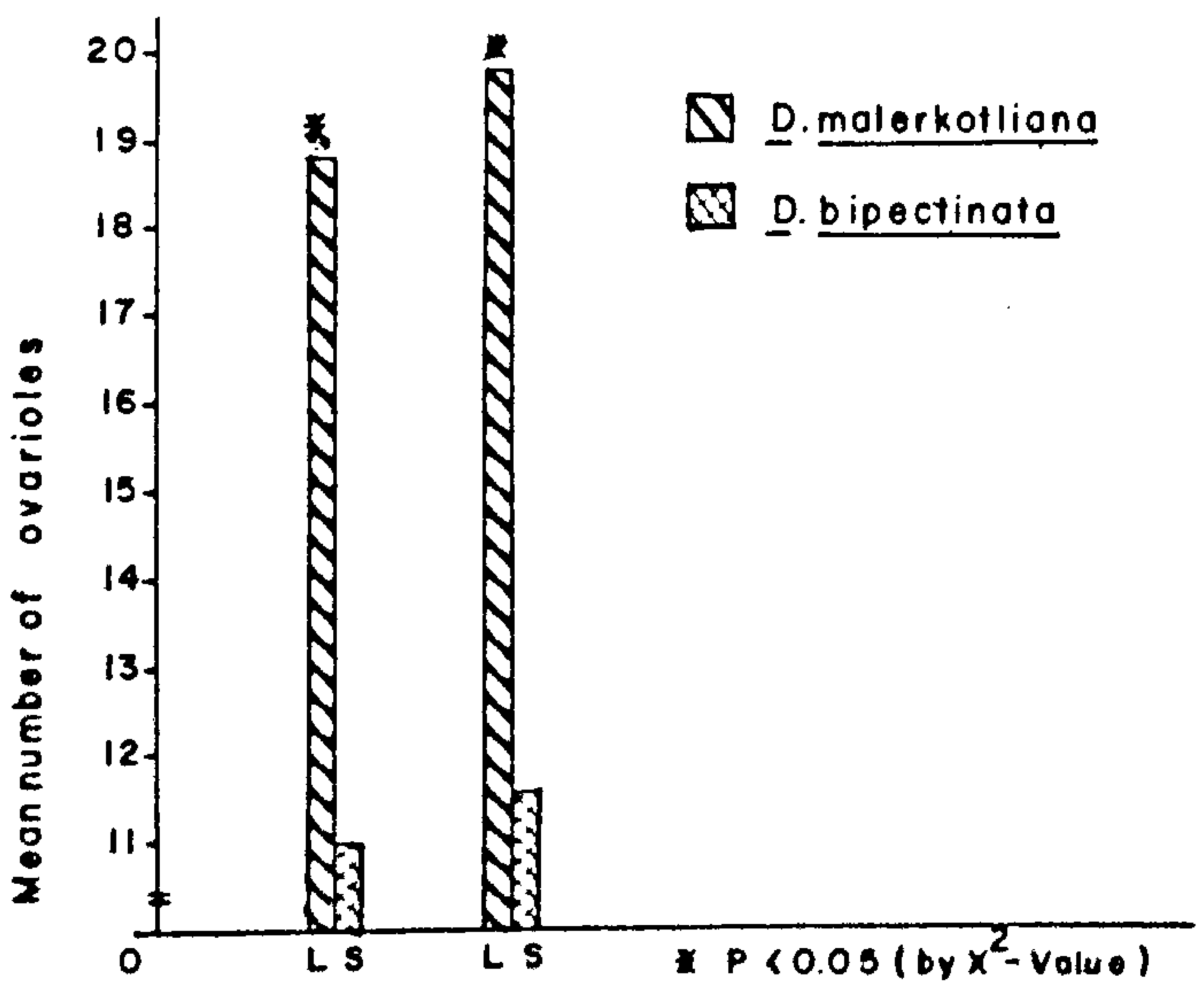

Figure 1. Mean number of ovarioles of large and small females. L, large female; S, small female.

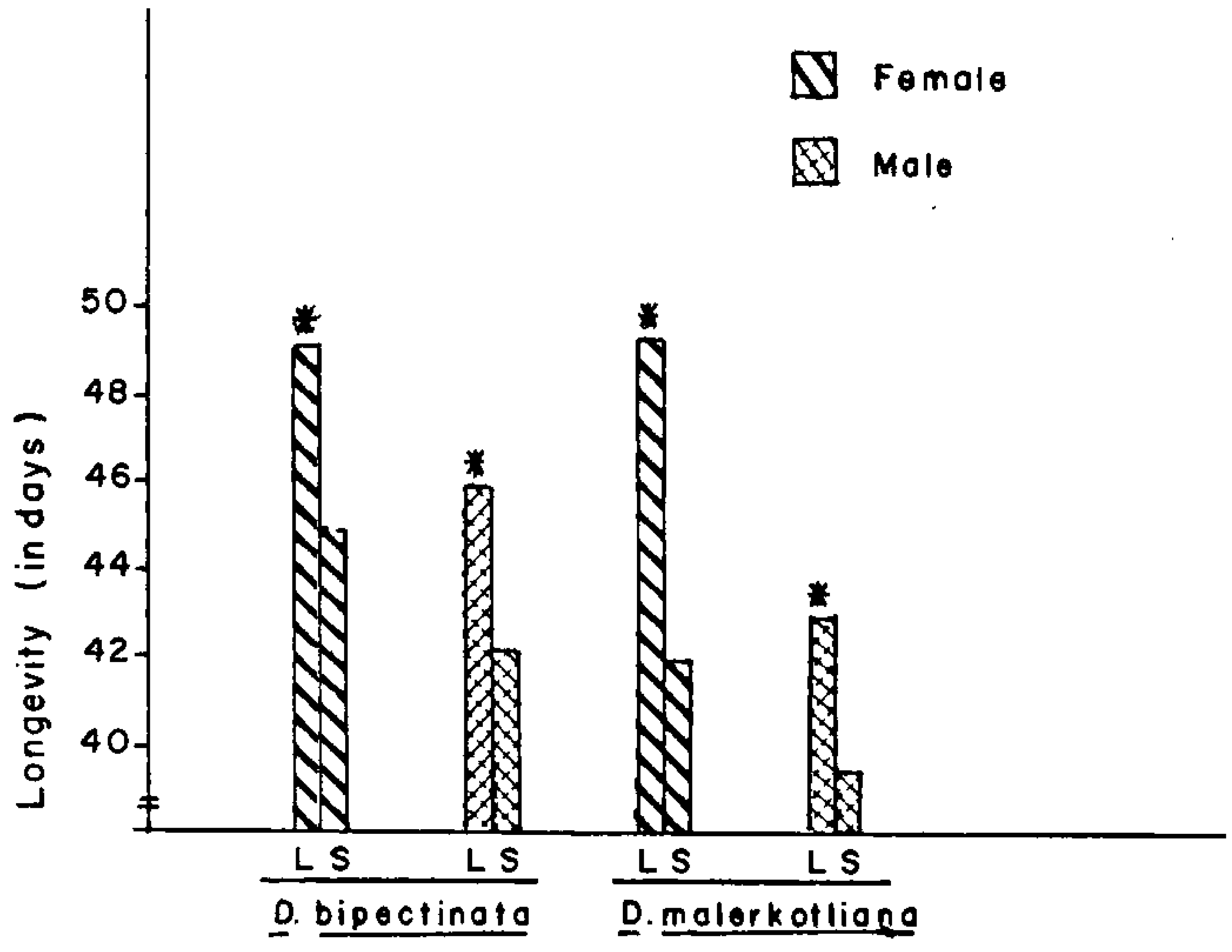

Figure 2. Longevity of large and small flies. L, large, S, small; *, $P < 0.05$ (by χ^2-value).

Higher reproductive success of large flies can also be accounted from its longevity. From Figure 2 it is clear that large flies have higher longevity than small flies in both *D. malerkotliana* and *D. bipectinata*. Partridge and Farquhar[11] have pointed out that larger males have been demonstrated to have greater longevity. In contrast to this we found both large male and female have greater longevity than small male and female. Large males with higher longevity could inseminate more females than small males and as a result the total number of progeny they produce is greater. Higher longevity of large females could also give an opportunity to mate with more number of males in their lifetime and produce more offspring than small female. Thus it is evident that the large males have higher reproductive fitness because they are able to mate more females by their higher remating ability compared to small males and they also have higher longevity than smaller males as a result of which they can inseminate more females in their lifetime than small males. Large females also have higher reproductive success because they have more number of ovarioles, lay more eggs and produce more fertile offsprings than the small female and also mate with more males in their lifetime than small female by having higher longevity.

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Deformational features in the river bluffs at Ter, Osmanabad district, Maharashtra: Evidence for an ancient earthquake

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Deformational features developed on the sedimentary sections at Ter, Osmanabad district in Maharashtra offer evidence for a spatially restrictive, but a damaging earthquake in the vicinity. The seismogenic features exposed in the sedimentary sections include flexures, warps, buckle folds and vertical offsets. Apparent trend of these structures suggests their formation under regional compressive stresses acting in the northeast-southwest direction. The radiocarbon age data obtained on the carbonaceous materials from the section indicate that the causative processes must have occurred ~1500 years ago. These structures, located 40 km northwest of Killari, the site of 1993 earthquake, add a new dimension to the question of spatio-temporal characteristics of earthquake generation in the Deccan Trap region.

OBTAINING evidence for past earthquakes is an important part in the seismic hazard evaluation of a region. This is particularly relevant in the shield regions where the historical seismicity data are meagre. And, most often these earthquakes recur at intervals longer than the recorded human history. Regions where large earthquakes have occurred in the recent years provide type areas to look for relics of past activity. Accordingly, we investigated several sites around Killari for possible indications of previous deformation[1–4]. One locale of interest was Ter which lies on the west bank of the river Terna, and is located 40 km, northwest of Killari and 18 km to the north-northeast of Osmanabad (Figures 1 *a* and *b*).

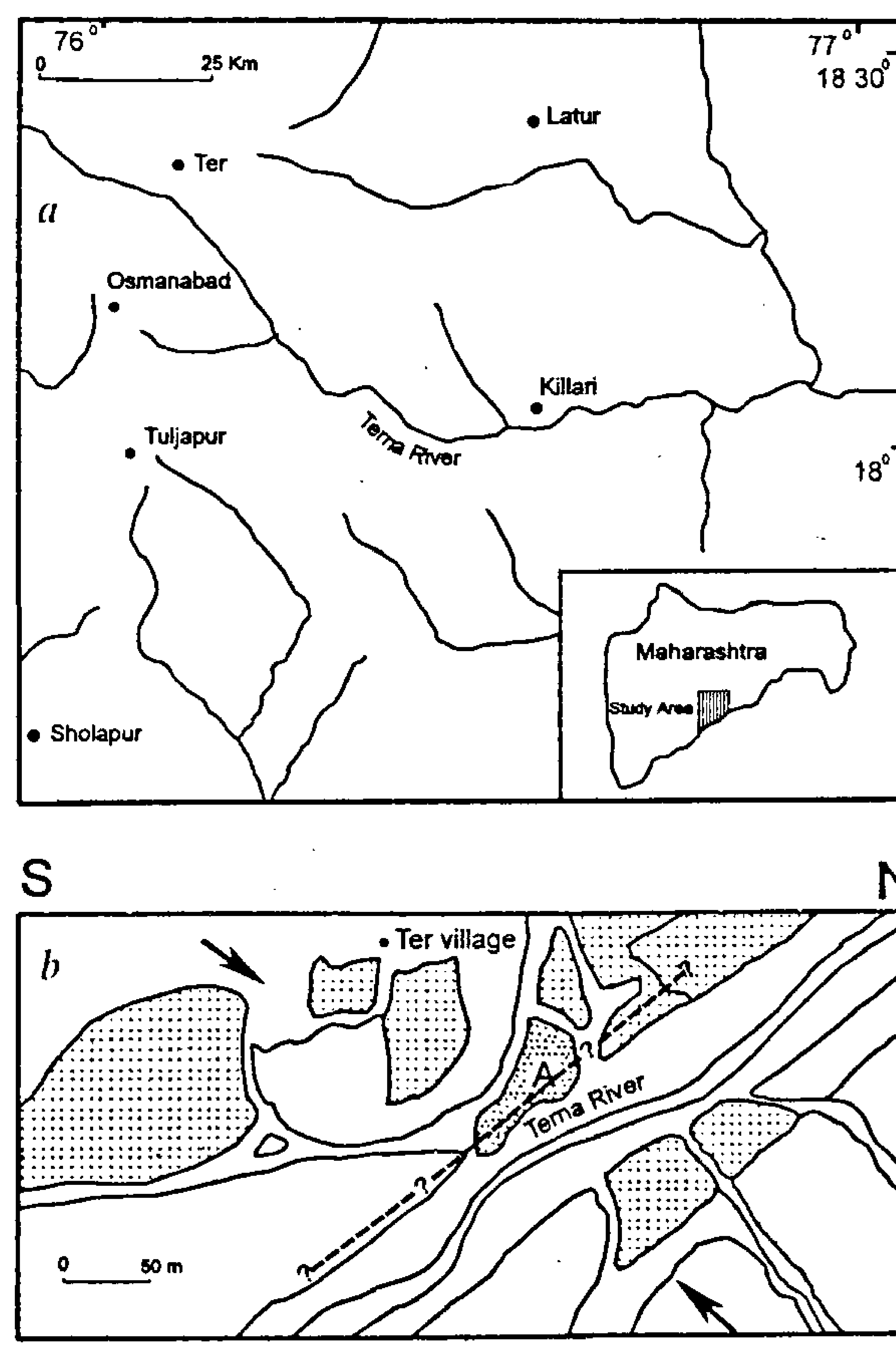

Figure 1 ***a***, Location map of the area; ***b***, Location of river bluffs at Ter. The section under study is denoted by 'A'. Arrows indicate direction of σ_1. Dashed line indicates probable trend of the seismogenic fault.