

toxigenic *V. cholerae* O1 strain no. 569B. These data indicate that the genetically engineered strains, including CVD 110 that lacks genes of all the known toxic factors, except NCT, produce a secretogen. Enhancement of secretory response upon passage suggests that if such a strain circulates in the community as is expected of a live oral vaccine, its virulence may increase further.

In the gel-diffusion test, 10-times concentrated culture filtrates of CT⁻ strain X-392 that produces NCT³ and the candidate vaccine strains gave a precipitin band against anti-NCT showing reaction of identity (Figure 1). This observation suggests that the secretogen produced by these strains is antigenically similar to NCT.

Volunteer studies using CT and Hly, or CT, Hly, Zot and Ace genes deleted mutant strains did not support the role of Hly or other toxic factors in the pathogenesis of cholera, since no difference in the ability to cause diarrhoea was observed between them and their parent strains¹. There is, therefore, every likelihood that the diarrhoeal episodes observed among the volunteers were due to the elaboration of NCT by the genetically engineered mutant strains. These observations indicate that vaccine strains produce the NCT and is supported by our earlier observation that anti-NCT completely neutralizes the enterotoxic activity of CT⁻ strains⁶, which has been demonstrated to produce the NCT.

The present results indicate that the candidate vaccine strains of *V. cholerae* O1, biotypes classical and El Tor, serotypes Ogawa and Inaba, are able to produce NCT even when the genes for CT, Hly, Zot and Ace are deleted and thus possess the potential to cause diarrhoea. These observations are important not only for our understanding of the pathogenesis and epidemiology of the disease but also for developing an effective candidate live oral vaccine strain against cholera.

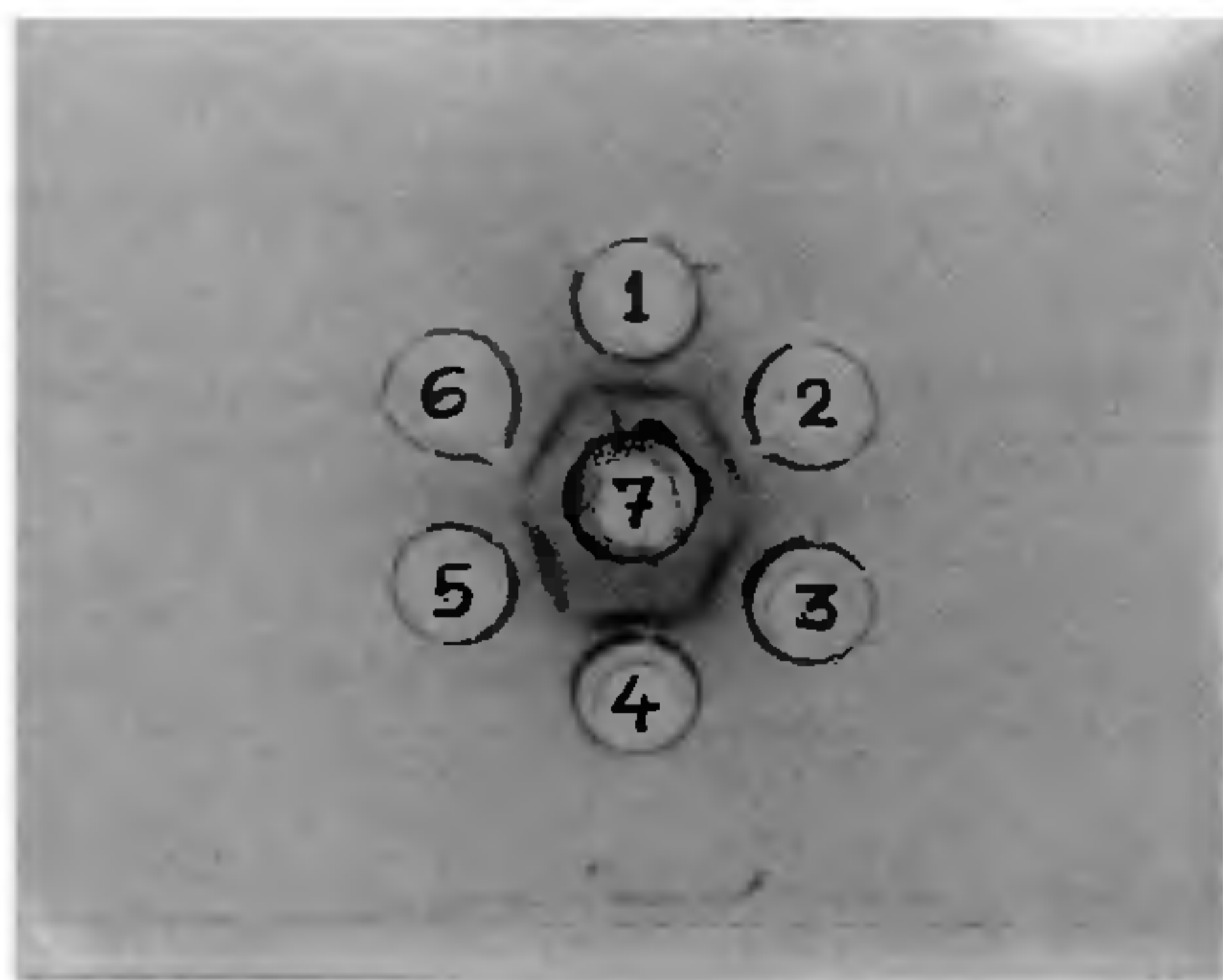


Figure 1. Immunological identity of the NCT with candidate live oral cholera vaccine strains. Ouchterlony immunodiffusion analysis of concentrated CF of CT gene-negative *V. cholerae* strain X-392 (well 1) and vaccine strains JBK 70 (well 2), CVD 104 (well 3), CVD 110 (well 4), CVD 101 (well 5), CVD 105 (well 6) against antiserum of X-392 enterotoxin (NCT) (well 7).

1. Trucksis, M., Galen, J. E., Michalski, J., Fasano, A. and Kaper, J. B., *Proc. Natl. Acad. Sci. USA*, 1993, 90, 5267-5271.
2. Tacket, C. O., Losonsky, G., Nataro, U. P., Cryz, S. J., Edlman, R., Fasano, A., Mickalski, J., Kaper, J. B. and Levine, M. M., *J. Infect. Dis.*, 1993, 168, 1536-1540.
3. Sanyal, S. C., Alam, K., Neogi, P. K. B., Hug, M. I. and Al-Mahmud, K. A., *Lancet*, 1983, 1, 1337.
4. Saha, S. and Sanyal, S. C., *FEMS Microbiol. Lett.*, 1988, 50, 113-116.
5. De, S. N. and Chatterjee, D. N., *J. Pathol. Bacteriol.*, 1953, 66, 559-562.
6. Saha, S. and Sanyal, S. C., *J. Med. Microbiol.*, 1989, 28, 33-37.

ACKNOWLEDGEMENTS. This study in part was supported by the Council of Scientific and Industrial Research, New Delhi in the form of Associateship to DVS and Senior Research Fellowship to AT.

Received 29 September 1995; revised accepted 9 January 1996

Deformation tectonics of the diffuse Indo-Australian plate boundary using centroid moment tensor data

N. Purnachandra Rao and M. Ravi Kumar

National Geophysical Research Institute, Hyderabad 500 007, India

The deformation tectonics of the Indo-Australian plate boundary has been fairly well explained by the Euler pole models. The Harvard centroid moment tensor (CMT) data concur with all the essential features described by these models. Additionally, it indicates the presence of widespread left lateral strike-slip faulting in the northern portion of the deformation zone from the Central Indian ridge up to the northern Ninety-east ridge, which incidentally is found to agree with the model of 'Wrench Fault Tectonics'. This is evidenced by the presence of focal mechanisms in this region with a consistent left lateral strike-slip faulting along NE-SW fault planes which are also continuous with the trend of the transform faults at the Central Indian ridge. However, it appears that this shearing phenomenon only complements the overall deformation process, but cannot explain it independently.

SEISMICITY in the north-eastern Indian ocean has for long been considered to be too high to be intraplate. Gutenberg and Richter¹ first reported this anomaly followed by other seismicity studies of this region²⁻¹³.

Sykes⁴ proposed the development of a nascent island arc between Sri Lanka and Australia to explain the unusual seismicity, which was refuted by later workers^{6,7}. Stein and Okal⁶ suggested a major left lateral strike-slip motion along the Ninety-east ridge as a result of greater resistance of the western part of the Indo-Australian

plate against the Himalayan continent-collision zone, as compared to the eastern part, which subducts smoothly beneath the Sunda arc.

Further evidence of relative plate motion between the Indian and Australian plates came independently from modelling of plate kinematics, using seafloor spreading, transform fault azimuth and earthquake slip vector data. The initial models of global plate kinematics assumed India and Australia to constitute a single plate¹⁴⁻¹⁶. Minster and Jordon¹⁶ showed that there were large misfits in the Indian ocean region. Stein and Gordon¹⁷ demonstrated statistically, that a great improvement in the fit could be obtained by splitting the Indo-Australian plate along a diffuse plate boundary zone. On the basis of a study of historical earthquakes, Wiens⁹ suggested that the diffuse plate boundary separating the Indian and Australian plates extends equatorially from the Central Indian ridge up to the northern Ninety-east ridge and further North, up to the Sumatra trench. The model depicts a relative plate motion described by convergence in general, in the deformation zone, and a left lateral strike-slip motion along the Ninety-east ridge. It has been further suggested^{8,10} that a combined Indo-Arabian plate separated from an Australian plate significantly improves the fit.

Using new data Gordon *et al.*¹⁸ demonstrated a sig-

nificant improvement over the model proposed by Wiens *et al.*⁸. The new Euler pole was located farther east of the earlier pole. As a result, the new model predicts a N-S divergence at the Chagos bank in addition to the N-S convergence in the east and a left lateral strike-slip along the Ninety-east ridge. The predicted rates of convergence across the deformation zone, however, are seen to be greatly reduced. Global plate motion modelling by DeMets *et al.*¹⁹ indicated similar results.

Using new aeromagnetic data of Carlsberg and Central Indian ridges, DeMets *et al.*²⁰ demonstrated a remarkable improvement in the understanding of the Indo-Australian plate kinematics. The existence of distinct, rigid Indian and Australian plates was unambiguously resolved. The uncertainty of the model and the extent of the diffuse boundary zone are thus highly constrained.

On the basis of seismic reflection and refraction studies in a portion of the deformation zone, Neprechnov *et al.*²¹ proposed a model of 'Wrench Fault Tectonics' for the north-eastern Indian ocean. In this model relative motion between the Australian and Indian plates is accomplished through left lateral shearing along NE-SW trending blocks in the deformation zone, in the direction of transform faulting from the Central Indian ridge towards the northern part of the Ninety-east ridge. This model, however, appears inadequate since it does not

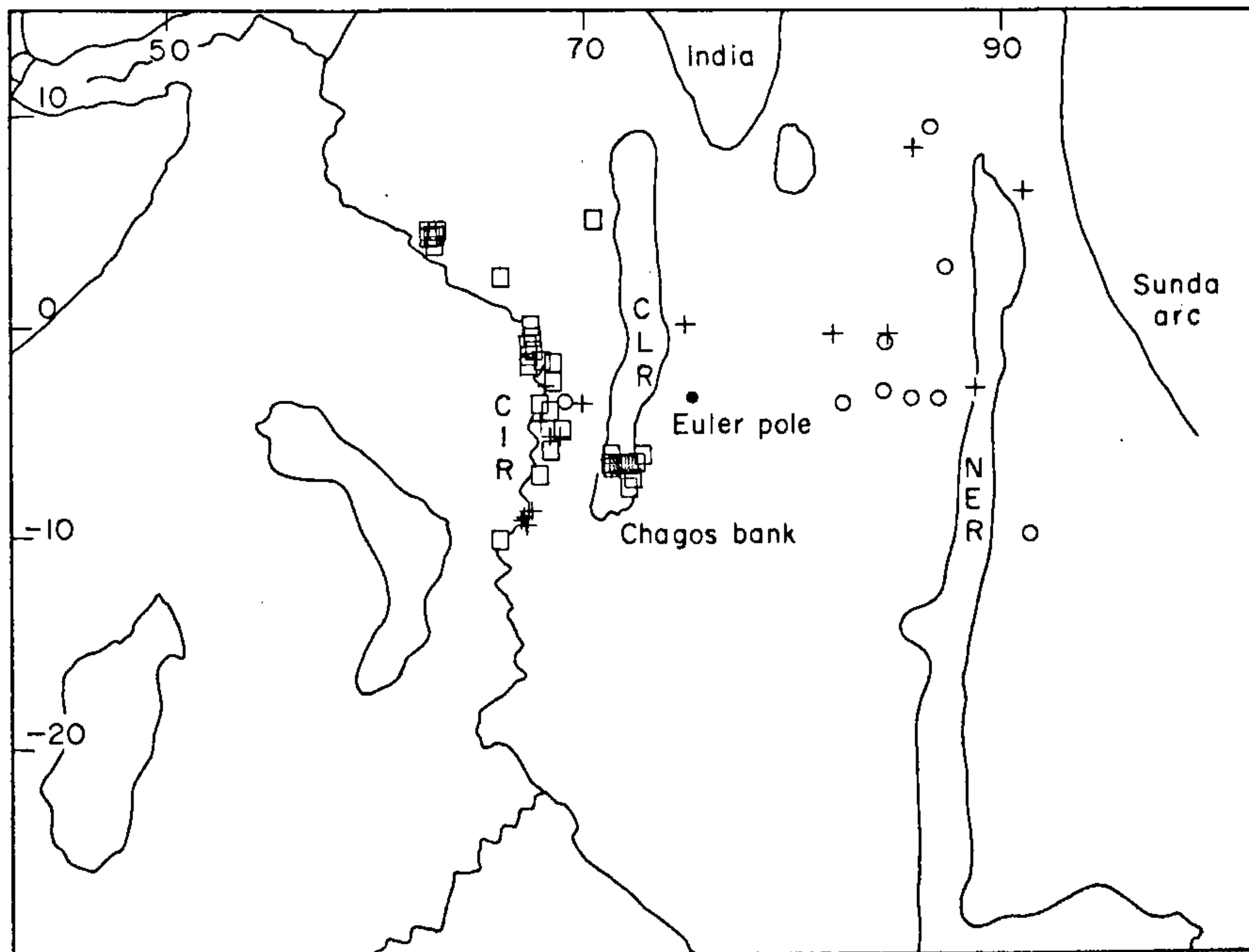


Figure 1. Seismo-tectonic map of the north-eastern Indian ocean showing the distribution of strike-slip (+), normal (□) and thrust (O) solutions. CIR, Central Indian Ridge; CLR, Chagos-Laccadive Ridge; NER, Ninety-east Ridge. (Modified after Wiens *et al.*⁸)

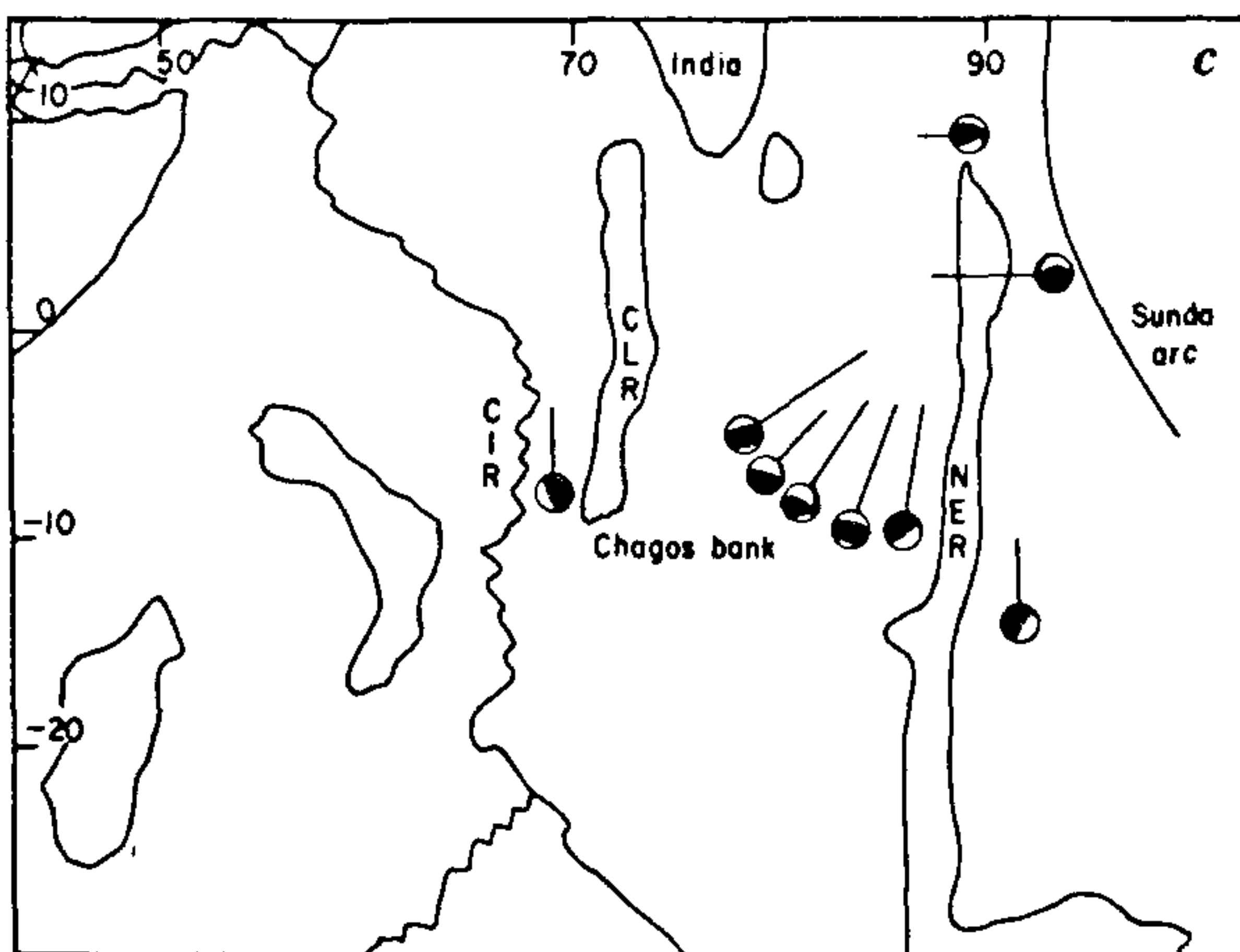
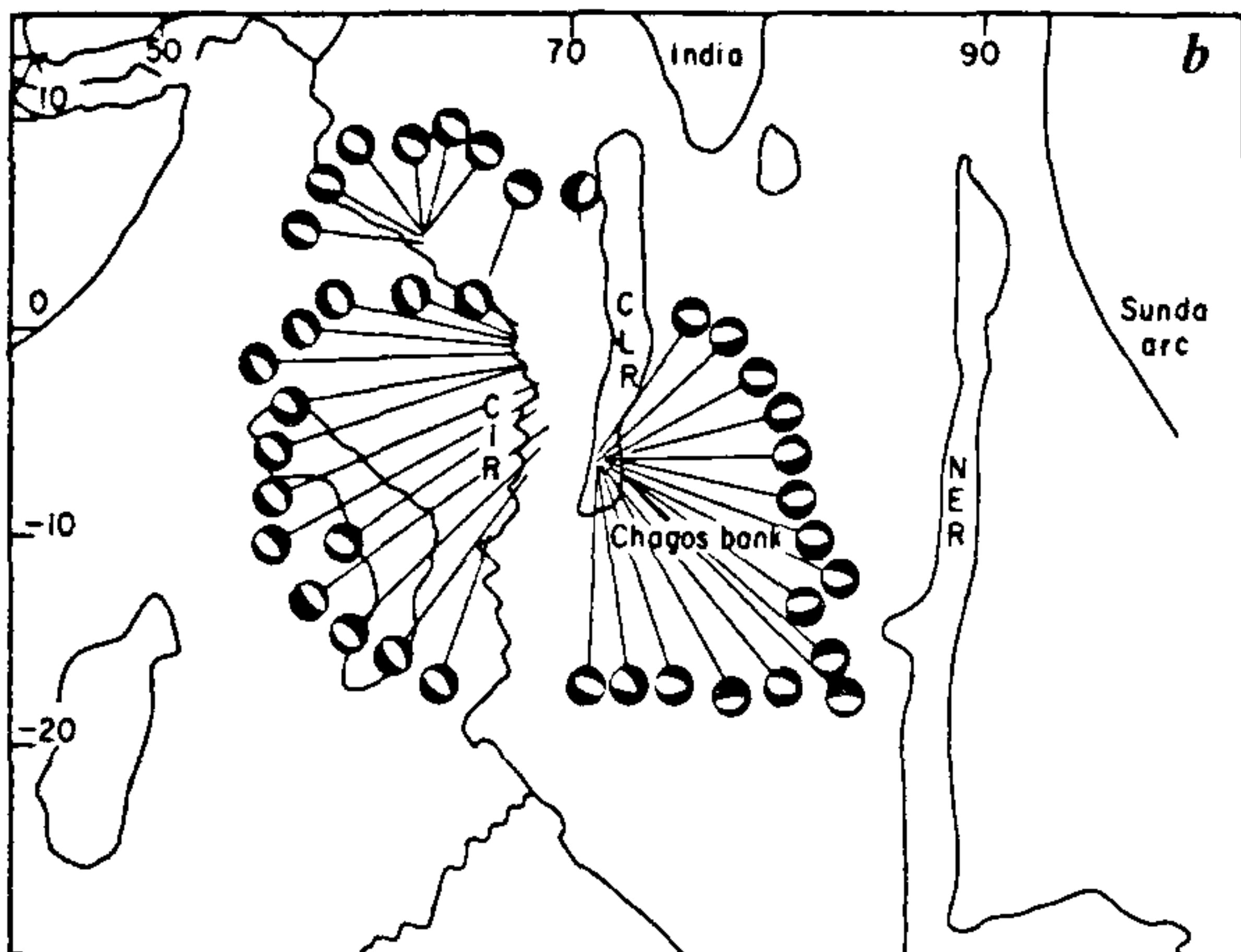
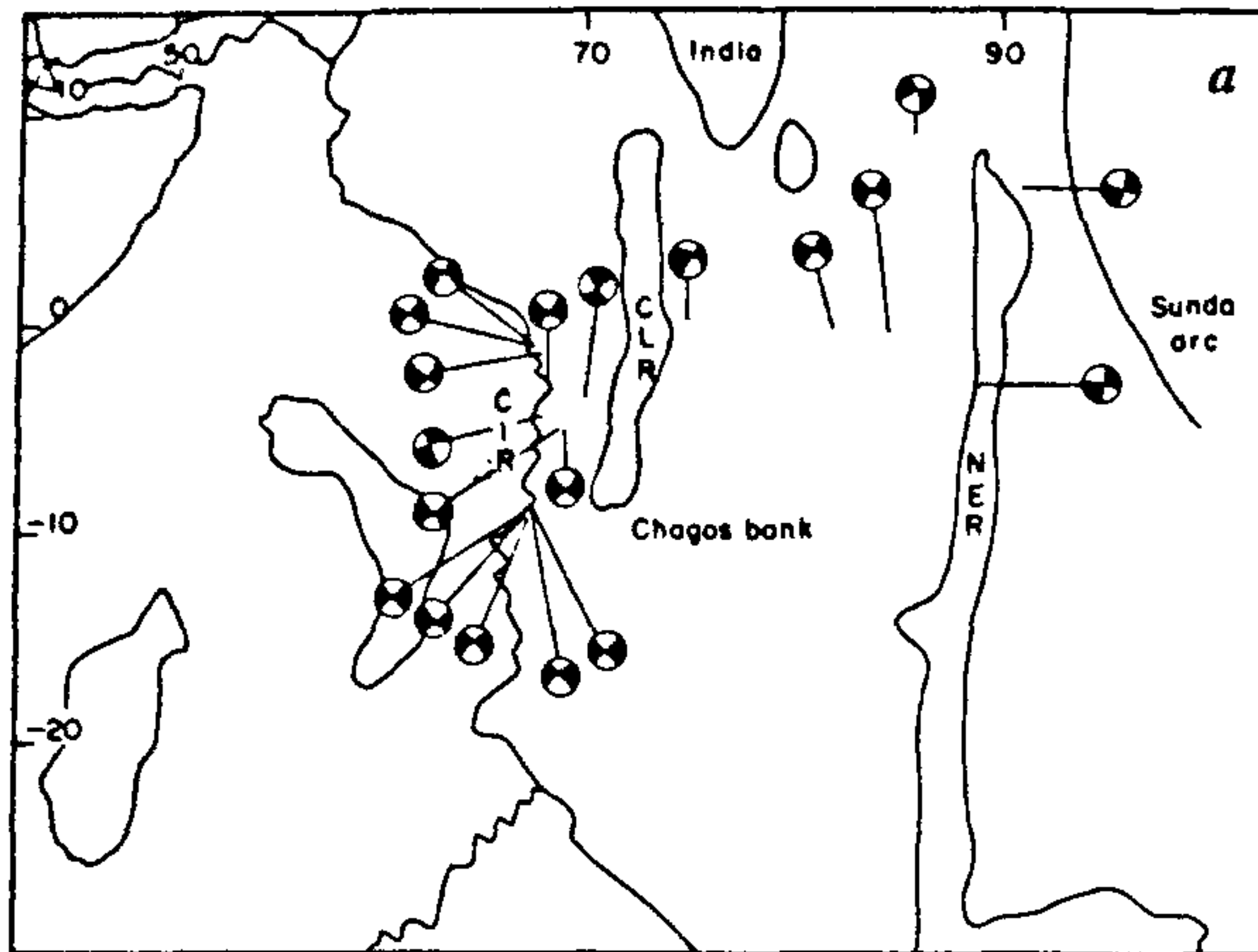


Figure 2. Focal mechanisms represented as lower hemisphere projections in the north-eastern Indian ocean. *a*, strike-slip; *b*, normal and *c*, thrust solutions.

account for the observed large scale convergence and divergence in the eastern and western parts respectively of the deformation zone, which are very well explained by the Euler pole models. However, evidence for the most salient feature of the model, namely strike-slip motion along the deformation zone in the NE-SW direction is seen, albeit in conjunction with the Euler pole model, as indicated in this study.

Other studies like gravity, bathymetry, seismic profiling and heat flow also indicate a diffused deformation zone with intense faulting and folding of sediments in approximately N-S direction^{11,13,21-25}.

In the present study, Harvard CMT solutions in the north-eastern Indian ocean region were analysed and their implications discussed in the light of existing hypotheses of the Indo-Australian deformation tectonics.

Sixty-six focal mechanism solutions of earthquakes from the Harvard CMT data in the north-eastern Indian ocean during 1977-92, were analysed. The data were classified into thrust, normal and strike-slip types, and separately examined, since this approach enables a better understanding of the style of deformation^{26,27}.

Figure 1 shows the distribution of 19 strike-slip, 38 normal and 9 thrust type solutions in the study region. The strike-slip solutions occur mostly in the northern part of the deformation zone, from the Central Indian ridge to the Ninety-east ridge. The normal solutions show two distinct clusters: one along the Central Indian ridge and the other at the Chagos bank. The thrust solutions mostly occupy the southeastern part of the deformation zone, west of the Ninety-east ridge. Absence of events between 75°E and 82°E is conspicuous. All these features are in agreement with the location of the India-Australia Euler pole given by Gordon *et al.*¹⁸ and later improved by DeMets *et al.*²⁰.

Focal mechanisms of the predominantly strike-slip, normal and thrust type solutions in the deformation zone are shown in Figures 2 *a*, *b* and *c* respectively. The tectonics of this region seems to be controlled mostly by the clusters of normal solutions at the Chagos bank and thrust solutions further east. The normal solutions at the Chagos bank, distinct from those on the Central Indian ridge, consistently indicate E-W oriented fault planes (corresponding to a N-S *T*-axis direction) while the thrust solutions in the east also indicate E-W fault planes (corresponding to a N-S *P*-axis direction) as shown in Figure 3. These two features are in good agreement with the divergence and convergence in the west and east respectively, as predicted by the Euler pole models. The strike-slip solutions on the Ninety-east ridge have NNE-trending planes in agreement with the strike of the ridge as well as with the known sense of left lateral slipping. The remaining strike-slip solutions are spread out with an approximately NE-SW alignment from the Central Indian ridge to the northern Ninety-east

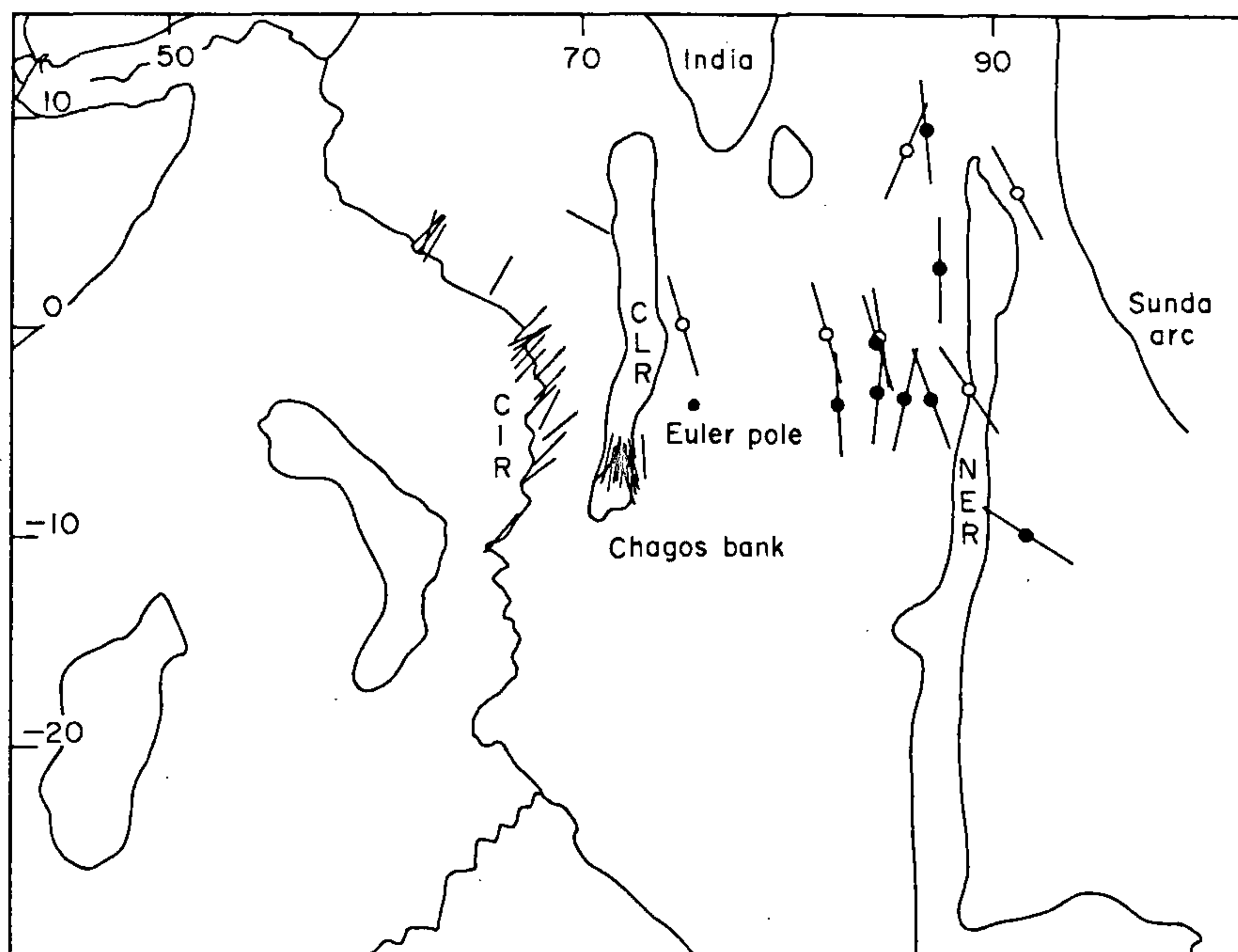


Figure 3. *T*-axis orientations of the normal solutions (short lines) and *P*-axis orientations of the thrust and strike-slip solutions (long lines with circles) in the north-eastern Indian ocean. Filled and unfilled circles represent thrust and strike-slip solutions respectively. (Strike-slip solutions along the CIR are not included.)

ridge, and seem to be in agreement with shearing proposed by Neprechnov *et al.*²¹. The supporting data, although sparse, quite consistently indicate NE–SW trending fault planes with a predominantly left lateral strike-slip motion (Figure 2 *a*). Evidence for such a shearing was also indicated by Gordon *et al.*¹⁸ although very few focal mechanism solutions were used. Also, their proposed direction of shearing is different (E–W to NE–SW) and is not substantiated by any other evidence. In this study, a correlation is brought out between these strike-slip solutions and the results of Neprechnov *et al.*²¹. It can be seen that these solutions are distinct from those close to the Ninety-east ridge which represent a different phenomenon. Further, these solutions are congruent with those on and close to the Central Indian ridge, both in style and sense of slip. They are also congruent with the known mechanisms of transform faulting at the ridge, indicating a continuation of the NE–SW trend of the transform faults into the deformation zone, in a left lateral shearing mechanism, as suggested by Neprechnov *et al.*²¹. In fact, the Harvard CMT data seem to provide evidence for such a shearing process coupled with rotation kinematics described by the Euler pole models.

The Harvard CMT data explain all the essential features

of the Indo-Australian deformation tectonics, as indicated by the Euler pole models. Further, it indicates partial operation of the ‘Wrench Fault Model’ of Neprechnov *et al.*²¹ described by left lateral strike-slip faulting in the northern part of the deformation zone, along NE–SW trending fault planes. Continuation of the transform faults from the Central Indian ridge into the deformation zone is suggested by the presence of strike-slip solutions all along, and their coherence in both, direction and sense of slip. This process, however, cannot by itself explain the deformation tectonics of this region as proposed by Neprechnov *et al.*²¹, but is understood to supplement the Euler pole rotation models given by Gordon *et al.*¹⁸ and DeMets *et al.*^{19,20}.

The contribution of the shearing phenomenon seems to be marginal because, although the focal mechanisms suggestive of wrench faulting are quite widespread, the sum of their scalar seismic moments is merely 1.5% of the total, with as much as 96% concentrated at the Chagos bank. The extension seen at the Chagos bank is, therefore, an important phenomenon in the deformation zone, which can be explained only by the Euler pole model. Also, the absence of observable offsets on the Chagos–Laccadive ridge indicates that wrench faulting in this region cannot be occurring on a large scale.

Several questions remain unanswered and detailed modelling studies would be required to completely understand the mode of deformation. The extremely high level of seismicity seen at the Chagos bank, remains an open question. The Euler pole models discussed, do explain the divergence at the Chagos bank, but fail to explain why normal faults are clustered here and not distributed west of the Euler pole. Further, the proximity of the Euler pole to this cluster of intense seismicity calls for an explanation. Verification of the model predictions can be directly made with the help of space geodetic techniques like Very Long Baseline Interferometry (VLBI), Satellite Laser Ranging (SLR) and Global Positioning System (GPS). The possibility of incipient subduction in the north-eastern Indian ocean cannot be ruled out, although the evidence at present is insufficient.

1. Gutenberg, B. and Richter, C. F., *Seismicity of the Earth and Associated Phenomena*, Princeton University Press, Princeton, 1954.
2. Stover, C. W., *J. Geophys. Res.*, 1966, **17**, 2575–2581.
3. Banghar, A. R. and Sykes, L. R., *J. Geophys. Res.*, 1969, **74**, 632–649.
4. Sykes, L. R., *J. Geophys. Res.*, 1970, **75**, 5041–5055.
5. Stein, S., *Geophys. J. R. Astron. Soc.*, 1978, **55**, 577–588.
6. Stein, S. and Okal, J., *J. Geophys. Res.*, 1978, **83**, 2233–2245.
7. Bergman, E. A. and Solomon, S. C., *Phys. Earth Planet. Inter.*, 1985, **40**, 1–23.
8. Wiens, D. A. *et al.*, *Geophys. Res. Lett.*, 1985, **12**, 429–432.
9. Wiens, D. A., *Earth Planet. Sci. Lett.*, 1986, **76**, 350–360.
10. Wiens, D. A., Stein, S., DeMets, C., Gordon, R. G. and Stein, C., *Tectonophysics*, 1986, **132**, 37–48.
11. Levchenko, O. V., *Tectonophysics*, 1989, **170**, 125–139.
12. Petroy, D. E. and Wiens, D. A., *J. Geophys. Res.*, 1989, **94**, B9, 12301–12319.
13. Levchenko, O. V. and Ostrovsky, A. A., *Phys. Earth Planet. Inter.*, 1992, **74**, 173–182.
14. Minster, J. B., Jordon, T. H., Molnar, P. and Haines, E., *Geophys. J. R. Astron. Soc.*, 1974, **36**, 541–576.
15. Chase, C. G., *Earth Planet. Sci. Lett.*, 1978, **37**, 355–368.
16. Minster, J. B. and Jordon, T. H., *J. Geophys. Res.*, 1978, **83**, 5331–5354.
17. Stein, S. and Gordon, R. G., *Earth Planet. Sci. Lett.*, 1984, **69**, 401–412.
18. Gordon, R. G., DeMets, C. and Argus, D. F., *Tectonics*, 1990, **9**, 409–422.
19. DeMets, C., Gordon, R. G., Argus, D. F. and Stein, S., *Geophys. J. Int.*, 1990, **101**(2), 425–478.
20. DeMets, C., Gordon, R. G. and Vogt, P., *Geophys. J. Int.*, 1994, **119**(3), 893–930.
21. Neprechnov, Y. P., Levchenko, O. V., Merklin, L. R. and Sedov, V. V., *Tectonophysics*, 1988, **156**, 89–106.
22. Eittreim, S. and Ewing, J., *J. Geophys. Res.*, 1972, **77**, 6413–6421.
23. Weissel, J. K., Anderson, R. N. and Geller, C. A., *Nature*, 1980, **287**, 284–291.
24. Geller, C. A., Weissel, J. K. and Anderson, R. N., *J. Geophys. Res.*, 1983, **88**, 1018–1032.
25. Chamot-Rocker, N., Jestin, F. and deVoogd, B., *Geology*, 1993, **21**, 1043–1046.
26. Rao, N. P., Kumar, M. R. and Chalam, S. V., in Proceedings of the 30th Annual Convention and Seminar on 'Space Applications

in Earth System Science', 21–23 December 1993, Indian Geophysical Union.

27. Kumar, M. R., Rao, N. P. and Chalam, S. V., *Tectonophysics*, 1995, in press.

ACKNOWLEDGEMENTS. We are grateful to Dr Harsh K. Gupta for constant guidance, useful discussions and a critical review of the manuscript. We thank Mr S. C. Bhatia for his useful suggestions. We also thank Dr A. M. Dziewonski for providing the Harvard CMT data required for this study.

Received 24 July 1995; revised accepted 28 December 1995

Influence of disturbance on fine root biomass and productivity in two deciduous forests of Western Ghats, Tamil Nadu

SM. Sundarapandian, S. Chandrasekaran and P. S. Swamy

Department of Plant Sciences, School of Biological Sciences, Madurai Kamaraj University, Madurai 625 021, India

The effect of anthropogenic disturbances on fine root biomass levels, net primary productivity (NPP) and distribution was studied in two deciduous forests of Western Ghats in Tamil Nadu, and it was found that the disturbances such as annual wild fire and cattle grazing enhanced the very fine root (≤ 1 mm) standing crop biomass and NPP. This could be due to the rapid re-occupation of land by a grass cover. Small scale disturbances such as canopy openings lowered the levels of very fine root biomass and NPP. This could be attributed to alteration in the edaphic environment. The marginal decline of fine root (> 1 to ≤ 3 cm) standing crop biomass and NPP may be because of mortality subsequent to the disturbance. Below-ground NPP showed seasonal variation during the study period. It has been concluded that the annual wild fire and cattle grazing enhances very fine root biomass and NPP, and also confirms the theory that the above-ground gap creates below-ground gap in deciduous forests.

UNDERSTANDING of the fine root dynamics is necessary for addressing important issues at several levels of resolution in biology¹. Greater proportion of the fine roots of many forests is located in the upper soil horizons and undergo rapid change due to disturbances. Anthropogenic disturbances create heterogeneity in edaphic environment. Very few studies have addressed the effects of disturbance on fine root dynamics in tropical forests. Raich² found similar amounts of fine root biomass in small, cleared plots after one year and