or the style[26]. The stochasticity in such a process can also bring out variations in petal-drop response.

It is possible that in self-compatible species with multi-ovulated, short-lived flowers like *Momordica*, genotype-specific induction of flower senescence may constitute an important aspect of plant reproductive biology, especially in the light of sexual selection. To evaluate the importance of these effects on pollination dynamics and fitness consequences, detailed field studies are however necessary.

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High biological productivity in the central Arabian Sea during the summer monsoon driven by Ekman pumping and lateral advection

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Open oceans are generally oligotrophic and support less biological production. Results from the central Arabian Sea show that it may be an exception to this. We provide the observational evidence of fairly high biological production (up to 1700 mg C m^{-2} d^{-1}) in the central Arabian Sea, along 64°E, during the summer monsoons of 1995 and 1996. The reasons for the observed high biological production, comparable to that from the traditionally well-known Somali upwelling region, were examined in light of the physical forcing and prevailing chemical fields. In the northern part of the central Arabian Sea, north of the axis of the Findlater Jet, upward Ekman pumping and entrainment driven by basin-wide winds along with advection of upwelled waters from the coastal region of Arabia supply nutrients to the upper layers. In the southern part, production is supported by nutrients advected from the Somali upwelling region.

CONVENTIONAL understanding of the Arabian Sea productivity, largely based on observations from the International Indian Ocean Expedition[1,2] (IIOE, 1959–65) and the Indian Ocean Experiment[3] (INDOEX, 1979), is that upwelling occurring along continental margins of Somalia, Arabia, and to a lesser extent, along the south-west coast of India during the summer (south-west) monsoon (ca. June–September) leads to high primary production. The general picture which emerged out of these studies was that during summer, the open waters of the Arabian Sea are oligotrophic (nutrient-depleted) and surface chlorophyll-*a* typically ranges from 0.1 to 0.5 mg m^{-3}, while primary productivity ranges from 100 to 500 mg C m^{-2} d^{-1} (refs 1, 2, 4). The lower ranges of these values are usually from the southern and eastern areas (ca. south of 15°N; east of 67°E). Subsequently, Pant[5] and Banse[6] also arrived at similar conclusions. However, satellite imageries[7] have shown higher surface pigment concentrations (> 0.5 and up to 2 mg m^{-3}) over larger areas up to 10°N. In the present study, we show that high production indeed occurs in the open (central) Arabian Sea, at least westward of 64°E, during

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*For correspondence. (e-mail: prasanna@csnio.ren.nic.in) summer and attempt to identify the source of nutrients from physical processes.

Under the Indian programme of the Joint Global Ocean Flux Study (JGOFS), CTD (conductivity–temperature–depth) was used to obtain profiles at one-degree interval[8] along 64°E, during the Spring Intermonsoon of 1994 (12 April–12 May; 11°N–21°N) and summers of 1995 (20 July–12 August; 11°N–18°N) and 1996 (3–25 August; 13°N–19°N). Water samples collected with CTD rosette were analysed for nutrients, chlorophyll-*a* and primary productivity measurements[9] (the latter, *in situ*). All measurements were made according to JGOFS protocols[10]. Due to rough weather conditions, biological measurements during summer 1995 were confined to 11°N in open waters.

During the 1994 Spring Intermonsoon along 64°E, column chlorophyll-*a* and productivity values were as low as 16 mg m^{-2} and 168 mg C m^{-2} d^{-1}, respectively (Table 1). In summer, these waters showed considerable increase in pigment concentrations (up to 60 mg m^{-2} and 1782 mg C m^{-2} d^{-1} at 15°N). High pigment and productivity values were observed both in the northern and southern areas. The production rates are comparable to those from the active upwelling areas off Somalia; ca. 1700 mg C m^{-2} d^{-1} in July–August 1979 (ref. 3) and 1200 mg C m^{-2} d^{-1} in July 1992 (ref. 11).

In Spring Intermonsoon, surface waters of the Arabian Sea (north of 11°N) was nutrient-depleted and at undetectable levels in the upper 50 m (ref. 8). But in the summer of 1995, a lens of high nitrate (~ 4 μM) was observed between 15°N and 17°N (ref. 12). This lens of water was 0.5°C colder as well as 0.1 psu (practical salinity scale) fresher than the ambient waters. In the summer of 1996 also, nitrate was about 1 μM in the upper 50 m to the north of 15°N (ref. 12). Interestingly, vertical profiles show that about 80% of the pigment concentrations and 85% of the production in summer occurred in waters of the mixed layer. The subsurface chlorophyll maximum (SCM) associated with the nitracline (~ 50–60 m), present during the Spring Intermonsoon, was not discernible in summer. Instead, higher chlorophyll and primary production was observed throughout the mixed layer indicating that nutrients were, in fact, available in the euphotic layer. Undetectable levels of nitrate in the surface layers of the southern region were presumably due to rapid biological uptake.

In order to gain an insight into the mechanisms that supply the required nutrients to promote production in summer, we analysed the prevailing physical conditions. During the summer of 1995, south-westerly surface winds showed a steady northward increase from 9 m s^{-1} at 11°N to about 17 m s^{-1} at around 16.5°N (the latter depicting the axis of the Findlater Jet along 64°E), beyond which wind speed reduced. Sea surface temperature (SST) decreased from 27.5°C at 11°N to 26.5°C at 16°N and increased further north. More significantly, mixed layer depth (MLD) decreased from about 100 m in the south to 45 m at 16.5°N (ref. 12). During the summer of 1996, the wind and MLD patterns were similar though wind with reduced speeds, increasing from about 6 m s^{-1} in the south to 13 m s^{-1} at 17°N and MLD decreasing from 110 m in the south to 42 m at 18°N were seen. On the contrary, thermal field during the Spring Intermonsoon was highly stratified with a uniformly thin (< 30 m) mixed layer and SSTs in excess of 29°C (ref. 12).

The nutrient input which supported the observed production and biomass in upper layers during summer, in contrast to the warm oligotrophic and highly stratified Spring Intermonsoon, obviously resulted from physical processes. These could be meso-scale eddies, wind-driven vertical mixing, Ekman pumping driven by positive wind-stress curl, the offshore advection of upwelled waters from the coastal areas or a combination of more than one of these processes.

Meso-scale, cold-core eddies could enhance production[13], by supplying nutrients to the upper layer through upwelling. We analysed the sea surface height maps of TOPEX/Poseidon altimeter (10-day snap shots) from November 1992 to August 1996 (ref. 14), which showed two anti-cyclonic circulation features (i) the Great Whirl centred around 9°N, and (ii) the Socotra eddy off Socotra island, during summer (June to August). The imageries, however, did not suggest the signature of any cold-core eddy in the vicinity of the sampling area

Table 1. Surface and integrated column (120 m) values of chlorophyll-*a* and primary productivity along 64°E during the 1996 summer monsoon. Measurements at 11°N were made in 1995. Values within parentheses are for 1994 Spring Intermonsoon and NA denotes, not available

	Chlorophyll-*a*		Primary production	
Latitude (degree N)	Surface (mg m^{-3})	Column (mg m^{-2})	Surface (mg C m^{-3} d^{-1})	Column (mg C m^{-2} d^{-1})
11	0.42 (0.04)	44 (9.2)	12.8 (0.7)	770 (163)
13	0.32 (NA)	26 (NA)	8.3 (NA)	792 (NA)
15	0.45 (0.05)	60 (16.6)	41.5 (0.8)	1782 (168)
17	1.12 (NA)	58 (NA)	8.9 (NA)	1029 (NA)
19	0.54 (0.03)	28 (9.0)	22.0 (NA)	830 (NA)

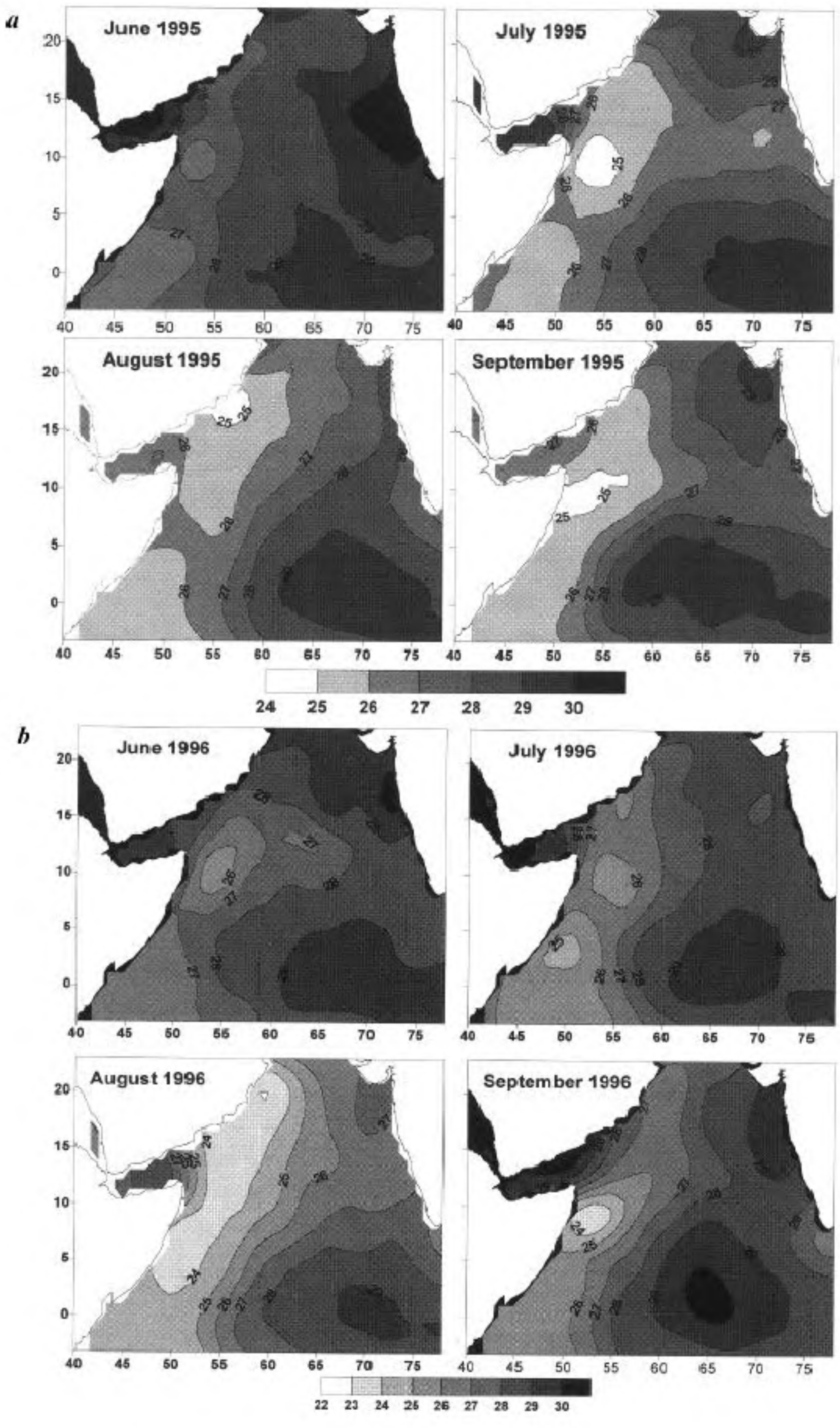

Figure 1. Monthly mean sea surface temperature derived from NOAA AVHRR data (see text) for June, July, August and September of (*a*) 1995 and (*b*) 1996. The grey-scale at the bottom indicates temperature in °C.

(along 64°E). Neither did satellite-derived SSTs during the summers of 1995 and 1996 (Figure 1) show the presence of eddies in the area of study.

High wind speeds during summer (on an average 15 m s^{-1}) in the Arabian Sea could result in large wind-driven vertical mixing (wind-stirring) and deepening of the mixed layer. The vertical mixing leads to entrainment of nutrient-rich waters from the thermocline region to the upper layers and this in turn could promote higher primary production. However, in the present observation, higher wind speed in the north did not lead to a deep MLD as one would expect; instead, it shoaled. Under lighter wind conditions, a shallow MLD was expected in the south, instead deep MLDs were observed. Hence, though the observed biological production could be explained by invoking wind-mixing, the observed meridional structure of wind and MLD along 64°E suggests processes other than/in addition to wind-mixing.

The northward shoaling of the MLD and possible upwelling of nutrients into the photic zone, in fact, could be explained by the indirect effect of wind. Bauer *et al.*[15] showed that cyclonic wind-stress curl (positive) occurring northwest of the Findlater Jet would induce a divergent Ekman transport in the upper ocean and drive open-ocean upwelling through upward Ekman pumping. In order to explore the nature and possible role of Ekman pumping in introducing nutrients from sub-surface, we used monthly mean FSU winds during 1995 and 1996 to compute the summer mean (June–August) wind-stress curl and Ekman pumping (taking into account the β-effect). In the summer of 1995, the wind-stress curl was positive north of 18°N along 64°E, extending up to about 23°N (Figure 2*a*). Similarly, the Ekman pumping velocities were also positive between 18 and 23°N along 64°E (Figure 2*b*). Distribution pattern was similar for the summer of 1996 as well (not shown). Both indicated that the basin scale winds induce an upward Ekman pumping under the cyclonic wind-stress curl, north of the wind-stress maxima. The vertical structures of nitrate and temperature in our observations do show a shoaling towards north, but reach depths up to 45 m only[12]. Incidentally, Levitus'[16] temperature climatology along 64°E also shows northward shoaling of isotherms (see right side of the box in Figure 3). All these suggest that Ekman pumping could be an important mechanism in transporting nutrients to the upper layers in the north. But the amount of nutrient upwelled into the euphotic zone and the thickness of the mixed layer would be controlled by the relative strength of wind-driven mixing (entrainment) and Ekman pumping. However, the lens of 4 µM surface nitrate between 15 and 17°N, which is detached from the deeper 4 µM isopleth (below 50 m)[12], suggests that this was not actually brought up from the subsurface, but from elsewhere. Thus, the productivity in the south should arise from nutrient input to the surface layers from an alternate mechanism.

Banse[4] proposed advection to explain the phytoplankton bloom off the Oman shelf, extending up to 65°E. Young and Kindle[17], in numerical studies using dissolved silicate as a passive tracer, advocated near-shore upwelling and offshore advection as an alternative mechanism to Ekman pumping, to explain the nutrient availability in the open-ocean region off Omani coast. McCreary *et al.*[18] based on a coupled, physical–biological model, suggested the role of eastward advection as secondary to entrainment as a source of nutrient in the central Arabian Sea during summer. More recently, based on AVHRR and TOPEX/Poseidon data, Manghnani *et al.*[19] showed that the southwest monsoon upwelled water off Oman coast is advected offshore in the form of plumes. In order to examine the role of lateral advection, we analysed monthly SST maps (1° × 1°) derived from AVHRR data during June to September

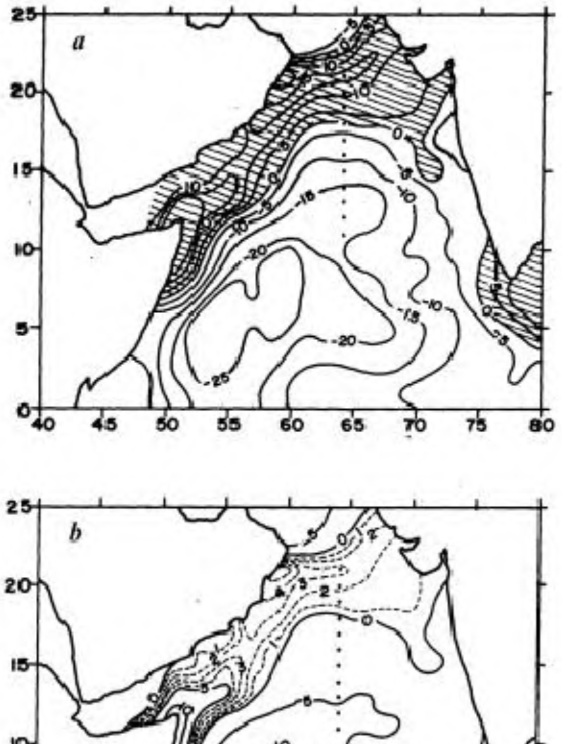

Figure 2. ***a***, Wind-stress curl (× 10^{-8} Pascal m^{-1}), and ***b***, Ekman pumping velocity (× 10^{-6} m s^{-1}) during summer of 1995 (see text for details). Stippled areas in (***a***) denote positive curl. Note the change in contour interval in (***b***) denoted by dashed contours, which indicate the region of upward velocity. Dark circles along 64°E denote the CTD stations.

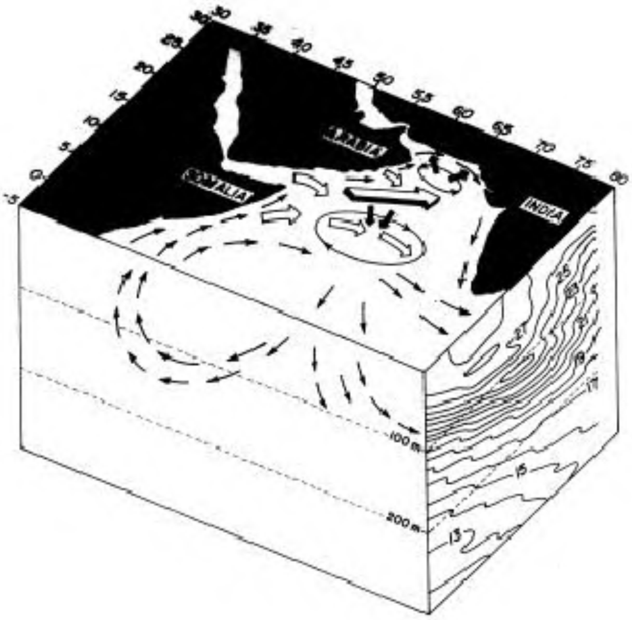

Figure 3. Schematic representation of the flow regimes and the physical forcing that fertilizes the central Arabian Sea during summer. Open arrows show the lateral advection from the Somalia and Arabia upwelling system, which transports nutrient-rich waters to the central Arabian Sea. Thin dark arrows show the prevailing flow in summer. Long open arrow with bold face is the atmospheric Findlater Jet, which extends from the tip of Somalia to Gujarat, India. The positive (negative) wind-stress curl north (south) of this jet drives the cyclonic (anticyclonic) circulation in the sea, which is indicated by the anticlockwise (clockwise) arrow; the dark, short arrows out of (into) it show the associated divergence (convergence). The right-hand side of the box shows the climatological mean thermal structure for August along 64°E (where the present measurements were made), based on Levitus'[16] data, which show the northward shoaling of isotherms.

for the years 1995 and 1996 (Figure 1), provided by PODAAC (Physical Oceanography Distributed Active Archive Center, for more information see, http://podaac.podaac.jpl.nasa.gov). Although there are a number of mechanisms that could produce cold SST along coastal regions, upwelling is most important during summer monsoon in the Arabian Sea. Hence movement of cold isotherms from coastal regions to offshore is an indication of advection of upwelled waters. The AVHRR SST field showed broad offshore transport from Somalia and Arabia during summer (Figure 1). With the onset of southwesterly winds along the Somalia coast during late May and early June, upwelling starts off Somalia and propagates northward. Upwelling enhances the nutrient levels in the coastal surface waters, but the swift Somali current[20] reduces the residence time of the upwelled water and hence primary productivity in this region remains far below potential[11]. The cold (17–22°C), nutrient-rich (nitrate typically ranges from 5 to 20 μM) upwelled water[3] steadily moves eastward, away from the coast under the influence of the prevailing easterly zonal currents. Similarly, nutrient-rich (~ 15 μM nitrate off Oman[21]) upwelled water from the Arabian coast also moves southeastward until August. The extension of this is seen up to 67°E.

In short, the observed high biological production in the central Arabian Sea is mediated by a combination of processes that vary from north to south of the axis of the Findlater jet. In the northern region, upward Ekman pumping and entrainment driven by basin-wide winds along with advection of upwelled waters from the coastal region of Arabia, supply nutrients to the upper layers. In the southern region, nutrients advected from the Somali upwelling region lead to fertilization. Figure 3 shows the schematics of the above-mentioned physical processes that are responsible for making the central Arabian Sea biologically productive during summer.

We used a simple calculation to see whether advection could transport enough nutrient out of the upwelling areas, to sustain the observed production. Based on a Redfield C/N ratio of 106/16 by atoms, a mean concentration of 0.2 μM nitrate over 60 m would sustain a production of ca. 1000 mg C m^{-2} in the upper 60 m (see also Veldhuis *et al.*[11]). At a typical advective rate of 28 cm s^{-1}, it takes about 30 days for upwelled waters of Somalia (ca. 57°E) to reach the central Arabian Sea (64°E). Assuming the biological uptake of nitrate at the rate of 0.2 μM per day, a nitrate concentration of about 6 μM at the source (upwelling region of Somalia) would be sufficient to be transported out to sustain the observed production. Since nitrate levels in the upwelled waters off Somalia are high enough, there would still be enough nutrients available for transport into the central regions of the Arabian Sea, even after considering loss from surface waters due to biological uptake.

Thus, we conclude that a large spatial realm, apart from the coastal waters and including central areas of the Arabian Sea, responds to physical and chemical changes during summer and translates to higher productivity than previously thought.

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Distinctive stomatal structure from dispersed leaf cuticle of Sindhudurg Formation, Ratnagiri District, Maharashtra, India

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Studies on dispersed leaf cuticle from Sindhudurg Formation of Miocene Age from Ratnagiri District, Maharashtra, India have revealed a unique kind of stomatal structure, not reported so far from any living or fossil plant group. The surface of the guard cells shows distinctly marked globular structures arranged in a row. The feature is consistent in all the stomata of the stomatiferous surface, but is not observed anywhere else on the lamina. The possibility of this character being genetically controlled cannot be ruled out. Additionally, the cells of the stomatiferous and non-stomatiferous surfaces of the leaf lamina show both xeromorphic and mesomorphic characters, indicating moderate climatic conditions between humid and dry. However, unicellular fungal spores frequently observed on the cell surface indicate a tropical, humid ecological condition.

CUTICULAR characters of dispersed fossil leaves are useful systematic evidences. Besides, they can also be used to characterize geological strata, build palaeocology and reconstruct palaeoenvironment. Moreover, certain specialized sculpturing of epidermal cells can also throw light on particular physiological functioning of leaves[1]. Dispersed leaf cuticles from Indian sediments are not reported so far. Maceration of lignitic samples from Sindhudurg Formation of Miocene Age from Ratnagiri District, Maharashtra has yielded well-preserved, dispersed leaf cuticles showing unusual stomatal microanatomical character in the form of globular structures arranged in a row on guard cells.

Geology of the Sindhudurg Formation has been worked out in detail by Saxena[2] (Figure 1*b*). The Formation was established for a sequence of clays with carbonaceous and lignitic seams occurring on the west coast of Ratnagiri and Sindhudurg districts of Maharashtra. Palaeobotanical information from this Formation is meagre. Nevertheless, a few workers have contributed to the knowledge of megafossils[3–11] and palynofossils[5,12–17] from these areas during the last two decades. Megafossils described are in the form of woods, fruits, sporangium and leaf cuticles.

The material was collected by one of the authors (A.A.) from lignitic beds exposed in a well at Vidya Mandir School (VMS) situated on Pawas Road about 8 km from PWD Guest House, Ratnagiri, Maharashtra (16°24′ North latitude and 73°24′ East longitude, Figure 1*a*).

In naming the dispersed fragments of leaf cuticle, we have adopted the artificial system of classification of dispersed cuticles devised by Roselt and Schneider[18], which is based on morphological features and was later followed by Kovach and Dilcher[19].

Anteterma Cellaratae (cuticle cellular)
Turma Anomorimatae (cuticle cellular with anomocytic stomata)
Subterma Disanomorae (cuticle cellular with dispersed anomocytic stomata)
Form Genus *Lusaticutis* Roselt & Schneider
Lusaticutis miocenica sp. nov. (Figure 2*a*, *b*).
Derivation of name: After the strata in which the species was found.

Leaf hypostomatic; cells of upper surface of leaf lamina differentiated into vein and mesh areas, main vein 4–9 cells wide, tertiary veins 2–3 cells wide, cells of mesh areas polygonal to irregular, irregularly arranged, cells of vein areas elongate polygonal, rectangular, squarish,

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