PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Macrofauna of the Intertidal Sand Flats on Low Wooded Islands, Northern Great Barrier Reef

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Macrofauna of the intertidal sand flats on low wooded islands, northern Great Barrier Reef

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[Plates 1 and 2]

An account of the macrofauna inhabiting the mobile substrata of the intertidal zone on low wooded islands in the Northern Region of the Great Barrier Reef Province is given. Excluding mangrove habitats, three main sediment–fauna types can be recognized: (i) well sorted sands forming the sloping beaches of sand cays, colonized by *Ocypode*, mesodesmatids and hippids; (ii) muddy sand flats supporting a very diverse fauna dominated in most areas by *Edwardsia* and chaetopterids; and (iii) areas of fine deposit, characterized by *Uca*, *Gafrarium* and *Marphysa*.

Some associations of animals, chiefly involving commensal polychaetes and bivalves, are described.

Introduction

A considerable amount of taxonomic and faunistic work has been carried out on the marine fauna of the Great Barrier Reef Province (early studies are reviewed by Dall & Stephenson 1953). Zoogeographically, the province, extending from about 9° 30′ S to 25 °S, is important due to its proximity to the Indo-Malayan area which is regarded as the faunistic centre of the Indo–West Pacific region (Ekman 1953). While our knowledge of the coral fauna and associated reef assemblages of such groups as the molluscs, echinoderms and fishes of the province is fairly extensive, other groups, such as the polychaetes, are poorly known. There is also a major gap in information concerning the detailed composition of the communities inhabiting the mobile substrata of both the littoral and sublittoral zones. The 1928–29 and 1954 Expeditions to Low Isles in the Northern Region (see Yonge 1930; Stephenson, Stephenson, Tandy & Spender 1931; Stephenson, Endean & Bennett 1958) carried out wide investigations of the reef's habitats and the resulting observations on the fauna of the 'sand flat' provide a useful basis for further ecological and faunistic studies.

During the second half of 1973, the Royal Society – Universities of Queensland Great Barrier Reef Expedition carried out geomorphological surveys of the low wooded islands north of 17° S, the latitude of Cairns (see Stoddart 1978). As a complementary study the author surveyed the communities inhabiting the intertidal sedimentary deposits on these islands. Although other islands and reefs were visited, this account is based chiefly on the observations made on low wooded islands between latitudes 14° 30′ S and 17° 00′ S, namely Low Isles, 16° 23′ S, 145° 34′ E (period of visit 23–30 August); East Hope Island, 15° 44′ S, 145° 27′ E (30 August–6 September); Three Isles, 15° 07′ S, 145° 25′ E (6–28 September); Two Isles, 15° 01′ S, 145° 27′ E (20–22 September); Nymph Island, 14° 39′ S, 145° 15′ E (9–10 October) and Ingram Island, 14° 30′ S, 144° 53′ E (22–23 October). In this area the tidal range is about 3.0 m at springs and 1.0 m at neaps (values for Cairns, Tide Tables, Department of Harbours and Marine, Brisbane).

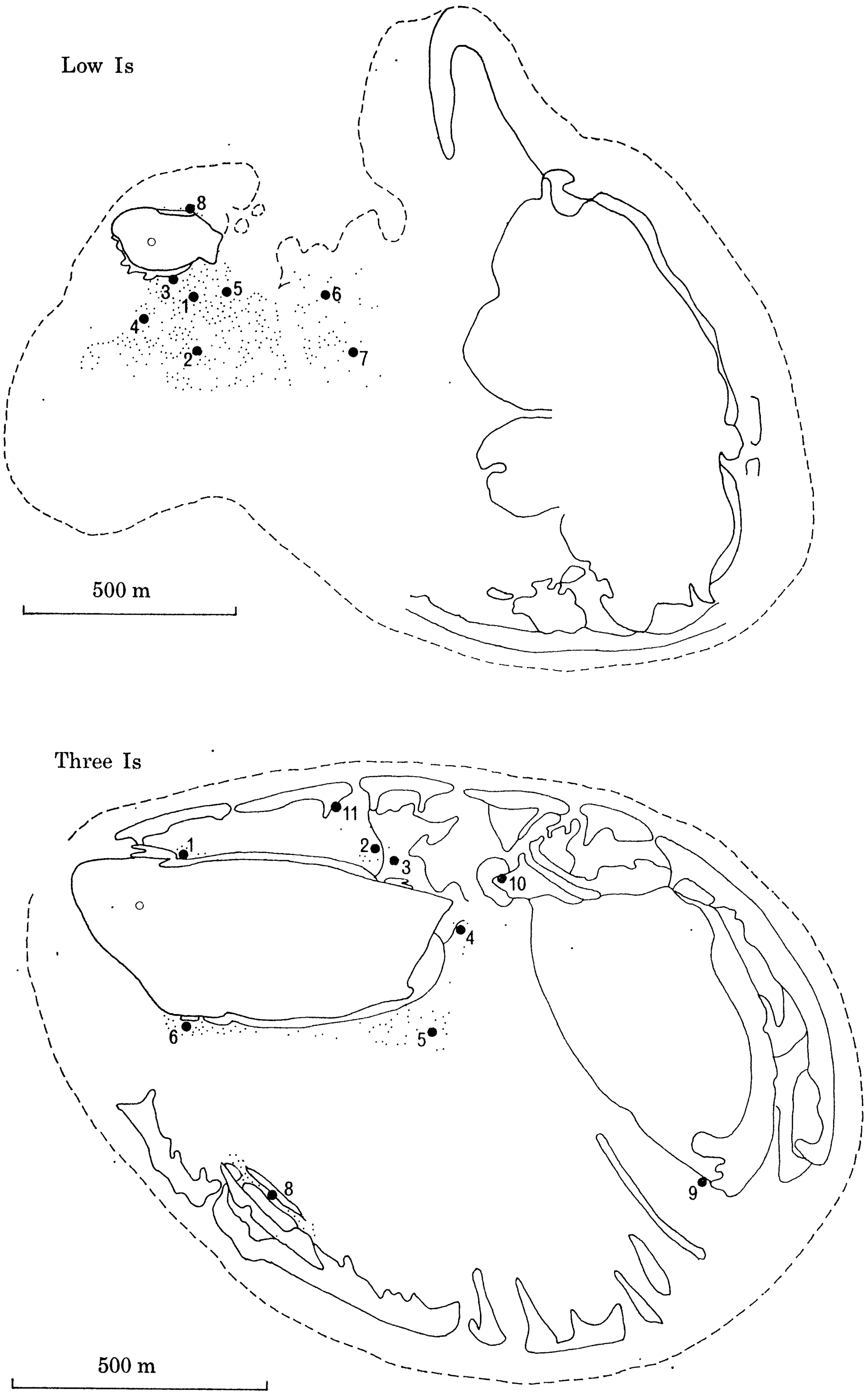

FIGURE 1. Maps showing locations of stations on Low Is (L1–L8) and Three Is (3.1–3.11). Outline features are based on the surveys of D. R. Stoddart.

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The geomorphological features of low wooded islands have been described by Steers (1929, 1930), Spender (1930) and Stephenson *et al.* (1931) (see also papers in this volume and part A of this Discussion). Typically, the central part of the reef complex, usually termed the reef flat (or 'pseudolagoon'), is covered by sediments composed chiefly of calcareous skeletal detritus derived from various reef organisms, notably corals, forams and algae (see Maxwell 1973; Flood & Scoffin 1978, part A of this Discussion), often with an admixture of fine material of indeterminate origin but including plant remains. The grading of the surface deposits is very variable, but generally black muds occur around the mangroves, poorly sorted muddy sands, often with a high proportion of coarse coral fragments, cover the reef flat, and well sorted, medium to coarse sands form the beaches of the sand cay. The depth of sediment on the reef flat varies from a few centimetres in hollows between areas of exposed rock, to 5 m or more (see Marshall & Orr 1931). On most low wooded islands, sea grasses colonize the sand flats, chiefly *Thalassia hemprichii* (Ehrenb.) Aschers. with *Enhalus acoroides* (L.f.) Royle, *Halophila* spp. and *Halodule* spp. (see Den Hartog 1970).

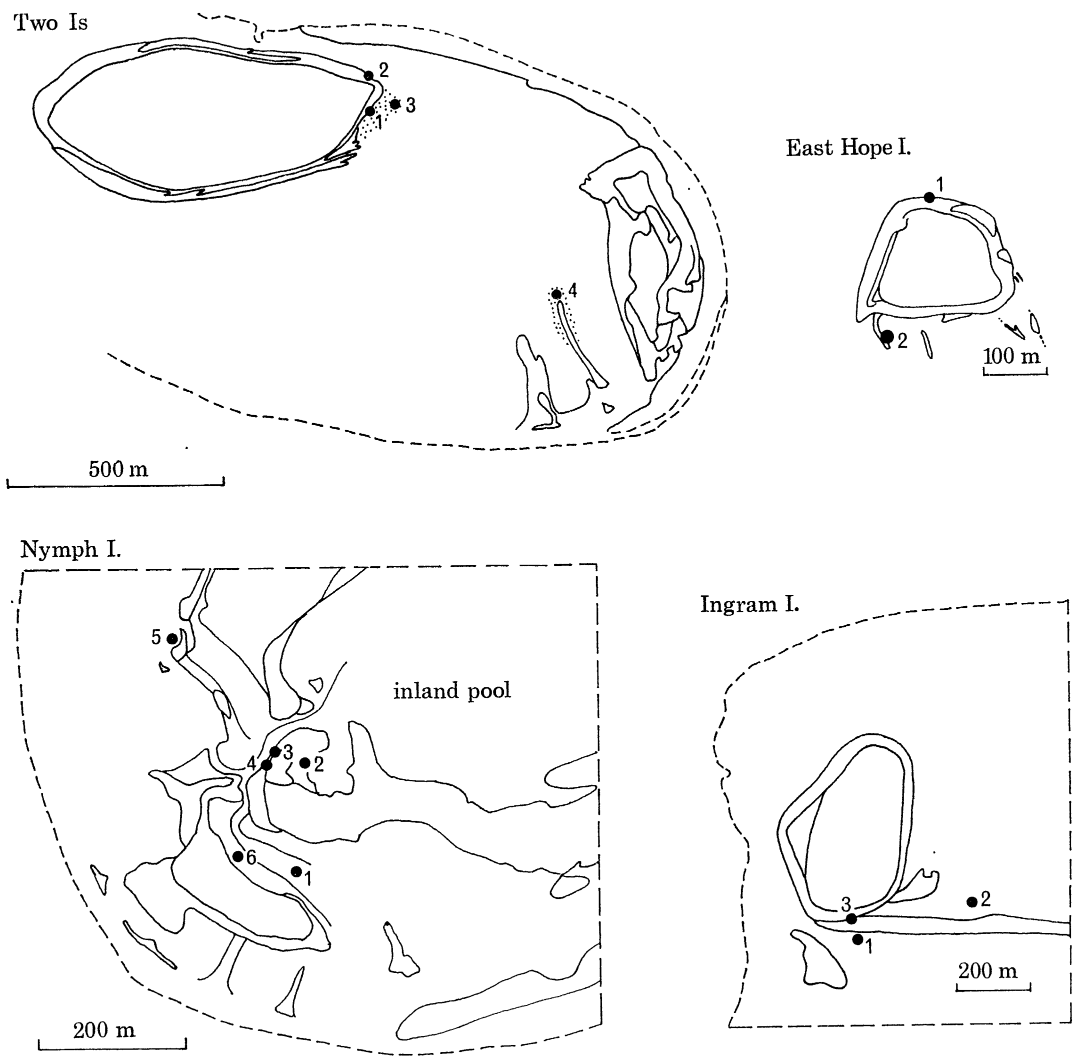

FIGURE 2. Maps showing locations of stations on Two Is (2.1–2.4), Nymph I. (N1–N6), East Hope I. (EH1–EH2) and Ingram I. (IN1–IN3).

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Qualitative samples of the macrofauna were collected in selected areas on the sand flats by digging, specimens being picked out by hand. Although extraction by sieving with 1.0 or 2.0 mm diameter mesh was possible in some areas, generally the presence of coarse coral debris in the deposits precluded this method. Foraminifera, which often compose a significant proportion of the deposit, were not collected since the reef forms are generally well known (see Collins 1958; Maxwell 1968). Drainage of the central reef flat area is often limited by the underlying rock formation and surface pools remain throughout the period of exposure. The resulting high water table makes excavation of the sediment to any appreciable depth impossible, and thus it is probable that some of the deeper burrowing species are not represented in the collections. However, the presence of some of these species can be recognized by their characteristic burrows, for example *Lysiosquilla maculata*. Where the sediment cover is thin, sampling is further complicated by the burrowing of many species into fissures in the underlying rock.

The positions of the infauna sampling stations are shown in figures 1 and 2. The surface burrowing forms, chiefly gastropods, were collected over wider areas, especially where their presence was indicated by surface tracks. Examination of material along the strand-lines on sand cays provided evidence of the presence of some rarer or inaccessible species, particularly deep-burrowing bivalves.

A systematic list of the species collected is given in table 1. Taxonomic work on the collections is still in progress and thus, at this stage, some names are provisional. Accounts of little-known species and groups are in the course of preparation. The major parts of the collections have been, or will be, deposited as follows: British Museum (Natural History) – Polychaeta, Crustacea, Echinodermata, Pisces; Australian Museum – Gastropoda, Galeommatidae; Western Australian Museum – Lamellibranchia; South Australian Museum – Sipuncula.

Table 1. Systematic list of species collected in the survey area from intertidal sedimentary deposits

See figure 1 for positions of stations. Generally distributed species are designated gen; species newly recorded for the province are marked †; mollusc species marked * or stations [ ] indicate records based on shells only.

Coelenterata	
Anthozoa	
Actinodendron plumosum Haddon	gen
Edwardsia gilbertensis Carlgren	gen
Edwardsia stephensoni Carlgren	3.3 IN1
Annelida	
Polychaeta	
Gastrolepidia clavigera Schmarda	gen
† *Lepidasthenia* sp. cf. *terrareginae* Monro	L2
† *Sthenelais zeylanica* Willey	L1 L6 L7
† *Bhawania pottsiana* Horst	L6 IN1
Eurythoe complanata (Pallas)	3.2 3.3
† *Pseudeurythoe paucibranchiata* Fauvel	L6 IN1
† *Phyllodoce* sp. cf. *fristedti* Bergström	3.1
Leocrates chinensis Kinberg	L1 EH2 3.3
† *Ophiodromus* sp. cf. *berrisfordi* Day	gen
† Syllid spp.	gen
Ceratonereis mirabilis Kinberg	3.3 3.11
† *Nereis* (*Neanthes*) *caudata* (delle Chiaje)	3.5
Perinereis cultrifera helleri Grube	3.3 3.11
Perinereis nuntia brevicirris (Grube)	IN3
Glycera gigantea Quatrefages	L1 L5 3.1 3.5 IN3
† *Glycera lancadivae* Schmarda	L3 3.1 3.4

TABLE 1 (*cont.*)

?†	*Diopatra* sp.	N1
†	*Onuphis* (*Nothria*) *holobranchiata* (Marenzeller)	L4 N1
	Marphysa mossambica (Peters)	3.8 3.10 N1 N2 N6
†	*Nematonereis unicornis* (Grube)	L1 3.5 N1 IN1
†	*Lumbrineris tetraura* (Schmarda)	gen
†	*Lumbrineris* sp.	L4 IN1
†	*Arabella iricolor* (Montagu)	EH1 EH2 IN1 IN2
†	*Arabella mutans* (Chamberlin)	gen
†	*Drilonereis major* Crossland	3.6 3.11
	Malacoceros (*Malacoceros*) *indicus* (Fauvel)	gen
†	*Malacoceros* (*Rhynchospio*) *glutaeus* (Ehlers)	3.5
†	*Scolelepis aitutakii* Gibbs	L5 IN1
†	*Scolelepis squamata mendanai* Gibbs	L3
†	*Magelona* sp.	L1
†	*Cirratulus* sp.	gen
†	*Cirriformia punctata* (Grube)	3.3 2.4
†	*Cirriformia tentaculata* (Montagu)	3.1 2.4
†	*Poecilochaetus tropicus* Okuda	L3
†	*Chaetopterus variopedatus* (Renier)	L6
†	*Mesochaetopterus sagittarius sagittarius* (Claparède)	gen
	Mesochaetopterus sagittarius subsp.	gen
†	*Phyllochaetopterus elioti* Crossland	gen
†	*Phyllochaetopterus* sp. cf. *brevitentaculata* Hartmann-Schröder	EH2
†	*Spiochaetopterus* spp.	gen
†	*Nainereis laevigata* (Grube)	3.3
†	*Scoloplos* (*Leodamas*) *chevalieri* (Fauvel)	N6 IN1
	Dasybranchus caducus (Grube)	gen
†	*Notomastus* sp.	2.4
†	Maldanid spp.	gen
†	*Owenia fusiformis* delle Chiaje	3.5 2.4 N5 IN1
†	*Myriochele* sp.	L1
†	*Euthelepus kinsemboensis* Augener	2.4
	Loimia medusa (Savigny)	gen
	Pista typha Grube	gen
†	*Sabella melanostigma* Schmarda	L2 L4 3.2
Sipuncula		
†	*Aspidosiphon gracilis* Baird	L6
	Aspidosiphon sp. cf. *tortus* (Selenka & de Man)	3.3
	Paraspidosiphon klunzingeri (Selenka & de Man)	L6 3.4 3.10 2.2 IN1
†	*Siphonosoma* (*Siphonosoma*) *rotumanum* (Shipley)	L8
	Siphonosoma (*Damosiphon*) *cumanense* Keferstein	gen
	Sipunculus robustus Keferstein	L2 3.6
Echiura		
	Anelassorhynchus sp. cf. *porcellus* Fisher	IN1
Mollusca		
Gastropoda		
	Chrysostoma paradoxum (Born)	L4
	Cerithium aluco (L.)	L3
	Cerithium vertagus L.	gen
	Ischnocerithium echinatum (Lamarck)	Three
	Rhinoclavis asper (L.)	gen
	Rhinoclavis sinensis (Gmelin)	Low
	Lambis truncata sebae (Kiener)	L4
	Strombus campbelli Griffiths & Pidgeon	L2
	Strombus gibberulus L.	gen
	Strombus luhuanus L.	L4 2.4
	Strombus variabilis Swainson	Low
	Natica gualteriana Recluz	Low 3.2
	Polinices aurantium (Roeding)	Low
	Polinices pyriformis (Recluz)	Low Three
	Sinum sp. cf. *planulatum* Recluz	2.2

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TABLE 1 (*cont.*)

Cypraea annulus L.	Low
Cypraea errones L.	Three
Cypraea moneta L.	Low
Nassarius albescens (Dunker)	Three
Nassarius coronatus (Bruguière)	gen
Nassarius luridus (Gould)	Low Three
Oliva annulata Gmelin	2.4
Oliva miniacea Roeding	3.2
Mitra mitra (L.)	L5 3.3
Vexillum vulpeculum (L.)	3.2
Melo amphorus (Solander)	L4 3.5
Conus arenatus Hwass	gen
Conus coronatus Gmelin	Three 2.4
Conus ebraeus L.	2.4
Conus eburneus Hwass	L4 3.2
Conus flavidus Lamarck	2.4
Conus pulicarius Hwass	3.5
Conus suturatus Reeve	Low EH2 3.5
Terebra affinis Gray	3.2
Terebra subulata (L.)	L5 2.4
* *Atys cylindricus* (Helbling)	[L1] [3.5]
* *Pyramidella sulcata* (A. Adams)	L5
Haminoea sp.	L4
?Aglajid sp.	IN2
Lamellibranchia	
Pinna muricata L.	L7
Anodontia (*Anodontia*) *edentula* (L.)	L4 IN1 [3.8]
* *Codakia* (*Codakia*) *punctata* (L.)	[Three-clay]
Codakia (*Codakia*) *simplex* (Reeve)	L2 [2.4]
Codakia (*Codakia*) *tigerina* (L.)	IN1 [3.8] [Three-cay]
Epicodakia bella (Conrad)	IN1
'*Devonia*' sp.	L5
'*Erycina*' sp. 1	IN1
'*Erycina*' sp. 2	L2 3.6
'*Erycina*' sp. 3	L5 L6 L7 2.4 IN2
Fronsella sp.	L5 IN2
'*Galeomma*' sp.	L3 L5
'Leptonid' sp.	L3
Phlyctaenachlamys lysiosquillina Popham	L2 L3 L5
Fimbria fimbriata (L.)	gen
* *Acrosterigma elongatum* (Bruguière)	[Three-cay]
* *Acrosterigma rugosum* (Lamarck)	[3.8] [Three-cay]
* *Acrosterigma subrugosum* Sowerby	[Three-cay]
* *Fragum* (*Fragum*) *fragum* (L.)	[Three-cay]
* *Fragum* (*Fragum*) *unedo* (L.)	[Three-cay]
* *Fragum* (*Fragum*) sp. cf. *dioneoum* Brod. & Sow.	[EH1]
Fragum (*Fragum*) sp. cf. *whitleyi* Iredale	L2 IN1
* *Mactra* (*Mactra*) *maculata* Gmelin	[Three-cay]
Atactodea glabrata (Gmelin)	gen (cays)
Davila crassula Deshayes	gen (cays)
Tellina (*Tellinella*) *virgata* L.	L4 2.2 3.4
* *Tellina* (*Cyclotellina*) *remies* L.	[Three-cay]
Tellina (*Quidnipagus*) *palatum* Iredale	[3.8]
* *Asaphis dichotoma* (Anton)	[3.8] [IN1] [Three-cay]
Gafrarium tumidum Roeding	3.8 N6
* *Gafrarium* sp.	[Three-cay]
* *Lioconcha* (*Lioconcha*) *castrensis* (L.)	[Three-cay]
Periglypta puerpera (L.)	3.5 [Three-cay]
Crustacea	
Lysiosquilla maculata (Fabricius)	gen
Alpheidae spp.	3.6 3.11

TABLE 1 (*cont.*)

?† *Axius* (*Neaxius*) sp. nr. *plectorhynchus* Strahl	gen
Callianidea sp.	L2 2.4
Hippa celaeno (de Man)	gen (cays)
Hippa pacifica (Dana)	EH1 3.6 2.1
Paguridae spp.	gen
Porcellana sp. nr. *ornata* Stimpson	L3
Albunea symnista L.	N1
Calappa hepatica (L.)	3.1 3.3 3.5 IN1
Thalamita admete (Herbst)	3.6
Thalamita crenata Latreille	3.3
Portunus sp.	3.5
Scylla serrata (Forskal)	N6
Leptodius exaratus (H. M. Edwards)	3.6
Pilumnus vespertilio (Fabricius)	3.6
?† *Tetrias* sp. affin. *fischeri* (A. M. Edwards)	L6
Pinnotheres sp.	L7
Ocypode ceratophthalma (Pallas)	gen (cays)
Ocypode cordimana Desmarest	gen (cays)
Macrophthalmus telescopicus (Owen)	L4 L5 L7
Uca tetragonon Herbst	gen (mud)
Uca sp.	N2 N3 N4
Mictyris sp. affin. *livingstonei* McNeill	N3
Echinodermata	
Asteroidea	
Archaster typicus Müller & Troschel	gen
Ophiuroidea	
† *Amphioplus* (*Lymanella*) *bocki* Koehler	L5 L6 L7 3.2
Amphiura diacritica H. L. Clark	L6
Macrophiothrix koehleri A. M. Clark	3.11
Echinoidea	
Laganum depressum Lesson	L5 L6
Maretia planulata (Lamarck)	L5
Schizaster lacunosus (L.)	L2
Metalia spatagus (L.)	L6
Metalia sternalis (Lamarck)	L6 L7
Holothurioidea	
† *Bohadschia bivittata* (Mitzukuri)	2.4
Bohadschia marmorata Jaeger	L3 2.4
Labidodemas semperianum Selenka	L3
Holothuria (*Halodeima*) *atra* Jaeger	gen
Holothuria (*Mertensiothuria*) *leucospilota* Brandt	gen
Holothuria (*Thymiosycia*) *arenicola* Semper	gen
Stichopus chloronotus Brandt	gen
Leptosynapta latipatina H. L. Clark	L1
Chiridota rigida Semper	L3 L7
Chordata	
Enteropneusta	
Balanoglossus australiensis Hill	gen
Balanoglossus carnosus (Willey)	gen
Balanoglossus studiosorum Horst	L7 N5
Pisces	
Leiuranus semicinctus (Lay & Bennett)	2.3
Callogobius sp. cf. *slateri* Steindacher	3.3
Cryptocentrus sp. cf. *leptocephalus* Bleeker	L1
Istiblennius meleagris Cuvier & Valenciennes	3.6
Carapus homei Richardson	L4

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Observations

The intertidal region of low wooded islands such as Low, Two and Three may be broadly divided into three main sedimentary areas; these are (1) the steeply sloping beaches of the sand cay composed generally of well sorted medium to coarse sands with coarser debris (see McLean & Stoddart 1978), (2) the flats of poorly sorted muddy sand and (3) areas of fine deposit accumulations (muds and silty fine sands) often colonized by mangroves, mainly *Rhizophora* and *Avicennia*. While the communities of the sand cay beaches and fine deposit areas consist of relatively few, often abundant, species, the sand flats support a very diverse fauna, but many of the species occur only as isolated individuals or appear to be very localized in their distribution. Although small areas are dominated by certain animals, such as *Mesochaetopterus* or *Balanoglossus*, in general there is no faunistic heterogeneity over large areas of the flats.

Sand cay beaches

The steeply sloping beaches of all sand cays appear to be colonized by the ghost crab *Ocypode*, its burrows occupying a zone from about the level of high water neaps to above high water springs. Random samples of *Ocypode*, mostly collected at night by torchlight, show that most populations are composed of the two widespread Indo–West Pacific species *Ocypode ceratophthalma* and *O. cordimana*, the former species being dominant.

The middle region of the slope is generally lacking in macrofauna species. Lower down, frequently in a narrow zone above the base of the slope at its junction with the flat, dense populations of suspension-feeding mesodesmatid bivalves are a common feature. Two species are represented, *Davila crassula* and *Atactodea glabrata*. Although the two species are often found separately, mixed populations occur in coarse sand and coral debris, and apparently their habitat preferences overlap. In the same situations, mole-crabs belonging to the anomuran genus *Hippa* are likewise abundant. These scavengers are principally *H. celaeno* (= *adactyla* Fabricius of earlier accounts; see Haig (1974)) but a few specimens of the larger *H. pacifica* are also to be encountered. This mesodesmatid–hippid association is particularly common on the northern shore of East Hope Island (Station EH1). Other macrofaunal species in this zone are few and include the eunicid *Arabella iricolor*. Occasionally, beneath beach-rock boulders embedded in the sand, *Perinereis* spp. can be found.

Sand flats

As stated above, the sand flat environment of the islands supports a very diverse assemblage of species, most of which are rare or only occasional. To illustrate this point, it might be mentioned that of the total of about 150 species recorded from the sand flats on the six islands of the survey (see table 3), about 70 are represented in the collections by one or two specimens only.

The surface burrowers are chiefly gastropods. The widely distributed forms *Cerithium vertagus* and *Nassarius coronatus* are the commonest everywhere, together with *Rhinoclavis asper*, *Strombus gibberulus* and *Polinices pyriformis*. Other cerithiids such as *Ischnocerithium echinatum* and *Rhinoclavis sinensis*, nassariids (*N. luridus* and *N. albescens*), naticids, such as *N. gualteriana*, and several *Terebra* spp. are less common and apparently more localized. A variety of both cypraeids and conids occur (see table 1); during daylight exposure periods, these are usually aggregated under coral boulders lying on the flats, as are various crustaceans such as portunids (*Thalamita* spp., *Portunus*), xanthids (*Leptodius*, *Pilumnus*), several pagurid spp. and a few alpheids. The ubiquitous polychaete *Eurythoe complanata* is also most frequently encountered under boulders but there is a notable absence of the large terebellid *Reteterebella queenslandia* Hartman, a conspicuous species in this habitat on southern reef flats such as Heron Island (Bennett, in Hartman 1963).

The deposit-feeding holothurians are the most conspicuous group of the surface fauna and *Holothuria atra* is ubiquitous on all islands, often mixed with fewer *Bohadschia marmorata*, *Stichopus chloronotus* and *Holothuria leucospilota*, the latter being much more abundant on the rocky areas of the reef flat. Another echinoderm, *Archaster typicus*, is also a common but less conspicuous inhabitant of the flats, its sandy coloration often partially concealing its presence as it lies half-buried in the sand during low tide.

Although specimens may be difficult to secure, the relative abundance of some species is clearly discernible from their characteristic disturbances of the sand surface or the mode of construction of burrows. The faecal casts of deposit-feeding enteropneusts are distinctive, recalling those of *Arenicola* on temperate shores (figure 3, plate 1). One of the largest species, *Balanoglossus carnosus*, is abundant on most sand flats, but is rarely taken intact, due to the soft, fragile nature of its trunk region. The volume and frequency of the casts of this species indicate considerable feeding activity during the ebb tide involving a significant turnover of the surface deposits. A smaller species, *Balanoglossus australiensis* (probably the *Ptychodera flava* Eschscholtz of earlier reports including Trewavas (1931)) is also common, especially in muddier patches, but the closely related *B. studiosorum* appears to be rare. A certain degree of particle selection in feeding has been demonstrated for some enteropneusts (cf. *Balanoglossus gigas* Fr. Müller; see Burdon-Jones 1962) and possibly the presence of these aggregations of *Balanoglossus* spp. causes local modifications of the sediment characteristics.

Where the depth of sediment is sufficient, the entrances to the extensive burrows constructed by the large stomatopod *Lysiosquilla maculata* can be found. As described by Yonge (in Popham 1939), the burrow entrance is partially sealed with a plug of mucus-bound sediment (figure 4, plate 1) which, when removed, reveals a circular, mud-lined hole, 6–8 cm in diameter extending vertically to a considerable depth. No specimens were captured nor even observed in the burrows at low tide (cf. McNeill 1968). Similar but smaller mud-lined burrows, 3 cm in diameter, often in depressions (figure 5, plate 1), are more frequent. These are excavated by the thalassinid *Axius* (*Neaxius*) sp. cf. *plectrorhynchus*. Single individuals can often be observed at the entrance to their burrow during low tide, and a total of eight specimens were caught by blocking their retreat with rapid thrusts of a fork. All of these animals (four males, four females) were taken from separate burrows and thus it is not known whether a pair of these shrimps occupies each burrow as in the case of *Neaxius* sp. on Aldabra (cf. Farrow 1971).

A further common and distinctive burrow, not identified, is illustrated in figure 6, plate 1; in this, the entrance, which is about 2 cm in diameter, is consolidated by coarse debris, mostly coral twigs. Often, gobies can be seen resting at the entrance at low tide, but these quickly withdraw on the slightest disturbance. Despite many attempts, only one goby was captured (*Cryptocentrus* sp. cf. *leptocephalus*). Possibly gobies construct these burrows or modify existing ones, as is done by *Cryptocentrus cristatus* (Macleay) (Ogilby, quoted in Marshall 1964), although other burrow-constructing fish, such as opisthognathids (see for example, Ogilby 1920; Eibl-Eibesfeldt & Klausewitz 1961) may be responsible. More probably these burrows may be constructed by alpheid shrimps since the accumulation of debris at the burrow entrance appears to be a typical habit of certain alpheids, and associations between these species and gobies have been described from widely scattered localities (Macnae & Kalk 1962; Farrow

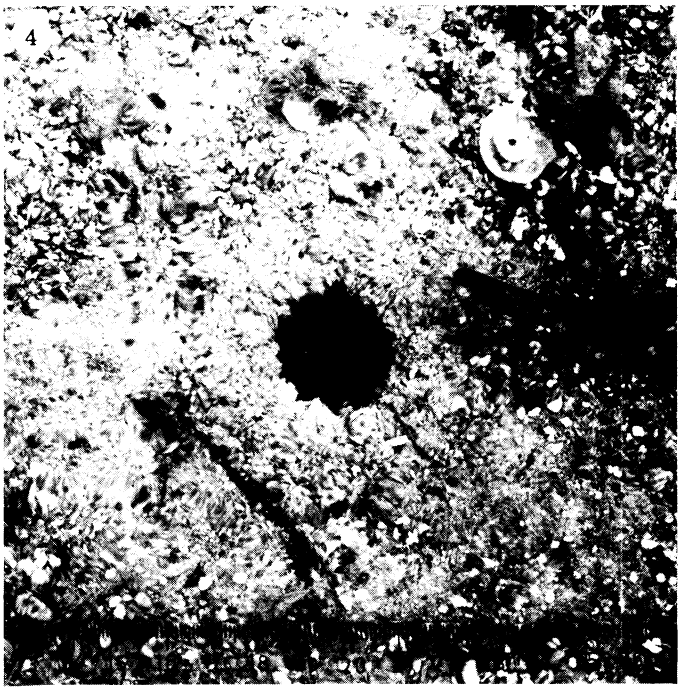
1971; Bayer & Harry-Rofen 1957). However, such associations do not appear to have been recorded from the Great Barrier Reef region.

As found by the earlier surveys of Low Isles, the infauna of these sand flats is dominated almost everywhere by the actiniarian *Edwardsia* (chiefly *E. gilbertensis*) and chaetopterid polychaetes. Previous accounts record only *Mesochaetopterus sagittarius* (= *M. minutus* Potts), but in fact two other genera, comprising at least three species, are also abundant; these are the robust *Phyllochaetopterus elioti* and the more delicate *Spiochaetopterus* species. Each of the three genera is readily recognizable by the appearance of the chitinous tubes which, when massed, effectively bind the sediment, frequently forming pronounced hummocks. This is particularly evident where dense aggregations of small *Mesochaetopterus sagittarius* are present (figure 7, plate 2), its intertwined sand-covered tubes maintaining a stable habitat for many smaller organisms such as the polychaetes *Myriochele* and syllid species.

A high proportion of the remaining infaunal species are also polychaetes (see table 1). Other tubicolous forms which are frequently encountered as scattered individuals are *Loimia medusa*, *Owenia fusiformis*, various, as yet unidentified, maldanids and *Pista typha*, the latter being commonest on Low Isles. A further species, *Sabella melanostigma*, occurs as isolated colonies, each consisting of three to five individuals. The commoner burrowing species include sedentariate forms such as *Malacoceros indicus*, *Cirratulus* sp. and *Dasybranchus caducus*, in addition to the errantiates *Glycera gigantea*, *G. lancadivae*, *Arabella iricolor*, *A. mutans* and *Lumbrineris tetraura*. Sipunculans were never taken in any numbers; the commonest is *Siphonosoma cumanense*, but *Sipunculus robustus* (= *S. angasi* Baird in Edmonds 1955), *Paraspidosiphon klunzingeri* (*sensu* Edmonds, 1956) and several *Aspidosiphon* spp. are also to be found. Echiura are poorly represented, only one specimen of *Anelassorhynchus* sp. cf. *porcellus* being taken.

In contrast to the mesodesmatids of the cay beaches, bivalves are surprisingly scarce on the sand flats. Excluding commensal species (see below), bivalves found living total only 21 specimens, comprising nine species, all of which appear to occur only as very dispersed individuals. These include *Fimbria fimbriata*, *Tellina virgata* and small specimens of the lucinids *Codakia* spp. and *Epicodakia bella*. Other species not found living but recorded through complete shells or single valves are more numerous, principally cardiids (see table 1).

To a large extent, burrowing echinoderms as a group have been overlooked in the region, with the notable exception of the widespread species *Holothuria arenicola*, which is commonly found on most flats. The sand flat on Low Isles supports an interesting selection of species, most of which appear to occur elsewhere only rarely in the intertidal zone. As found by the earlier surveys, around the Anchorage on Low Isles (Station L5), a good low spring tide uncovers fairly numerous populations of the clypeastroid *Laganum depressum* (including *L. dyscritum* Clark, 1932), and the spatangoid *Maretia planulata* (see Endean 1956). The latter species, which is a common sublittoral form, was observed coming to the surface of the sand in late afternoon before immersion by the incoming tide (figure 8, plate 2), presumably a response to low oxygen conditions. Such behaviour has also been described for this species at Lindeman Island by Ward (1965, as *M. ovata*). Three other spatangoids can be dug, namely *Schizaster lacunosus*, *Metalia spatagus* and *M. sternalis*, but all are seemingly rare since in each case only one or two specimens were uncovered. Two burrowing ophiuroids collected on Low Isles are of particular interest, namely *Amphiura diacritica* and *Amphioplus* (*Lymanella*) *bocki* (see below). Both of these amphiurids burrow to a depth of 8–10 cm, with the body disk lying in a cavity and arms extended towards the surface in a manner similar to that described for other members of the family



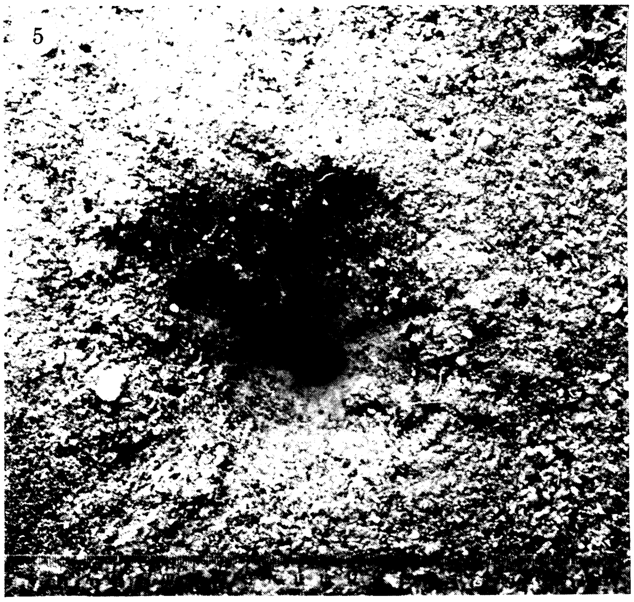


FIGURE 3. The faecal casts of the enteropneust *Balanoglossus carnosus* on the sand surface at low tide. Scale = 30 cm. Low Isles, Station L1, 27 August.

FIGURE 4. The entrance to the burrow of the stomatopod *Lysiosquilla maculata*. Low Isles, Station L1, 27 August.

FIGURE 5. The entrance to the burrow of *Axius* (*Neaxius*) sp. Low Isles, Station L1, 27 August.

FIGURE 6. The entrance to the burrow of ? alpheid sp. Low Isles, Station L2, 27 August.

(*Facing p.* 90)

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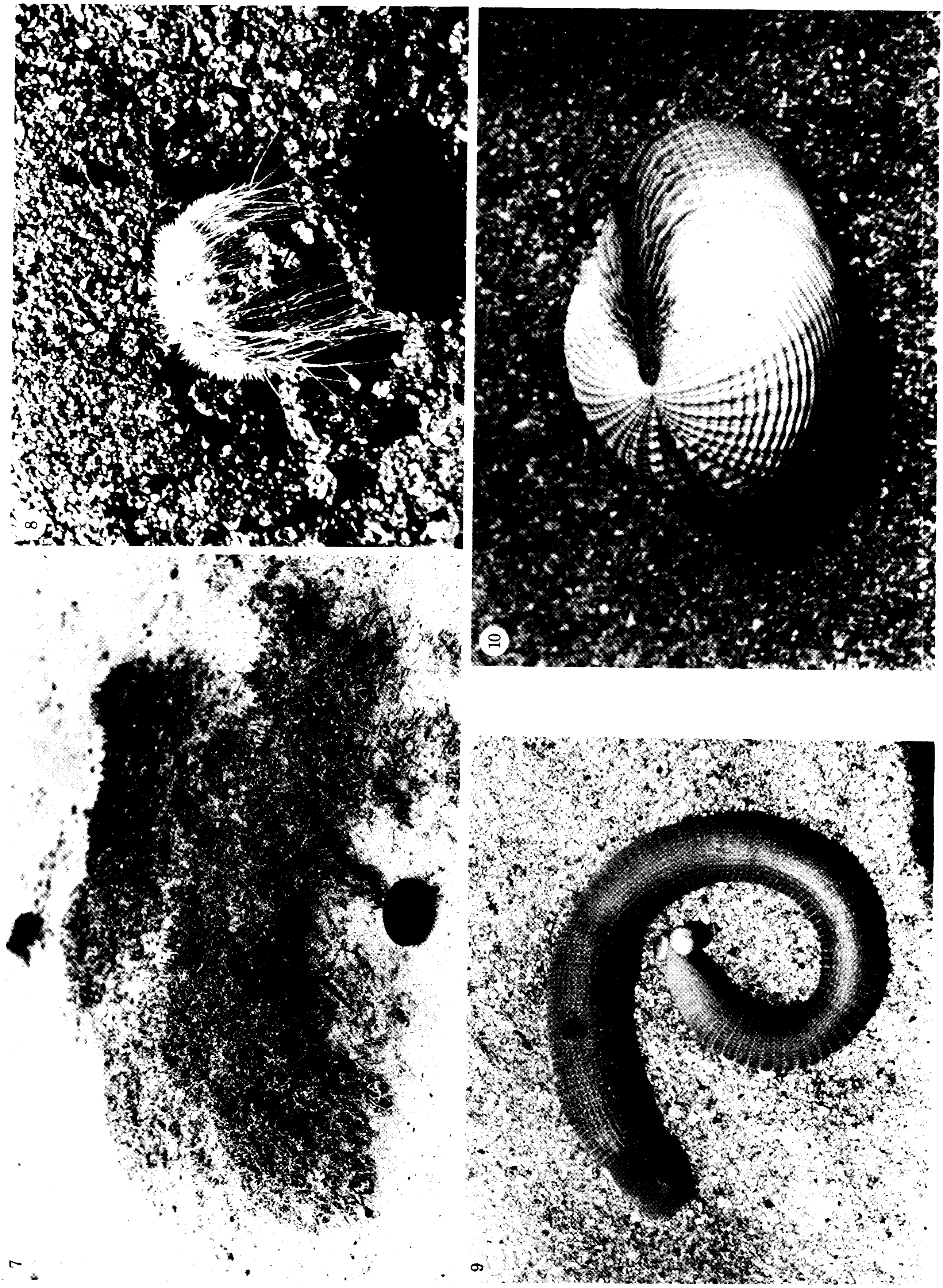

FIGURES 7–10. For description see opposite.

(see Des Arts 1911; Mortensen 1927). The smaller burrowing holothurians, such as *Leptosynapta latipatina*, *Labidodemas semperianum* and *Chiridota rigida* all appear to be uncommon in the survey area although the latter two species are both widespread in Queensland waters (see Endean 1957).

Fine deposit areas

Areas of fine sediment (muddy and silty fine sands) were not surveyed extensively and no attempt was made to study the fauna of mangrove muds, although a comparison of the latter with that found on the mainland (see Macnae 1967) would prove instructive. However, where investigated (i.e. Stations 3.8, 3.9, 3.10, N6), fine deposits contain relatively few species characterized by the fiddler crab *Uca tetragonon*, the venerid *Gafrarium tumidum* and the eunicid polychaete *Marphysa mossambica*. Several other more widely distributed species also extend to these areas, namely *Dasybranchus caducus*, *Malacoceros indicus* and the occasional sipunculan (*S. cumanense* and *P. klunzingeri*). Complete shells of deep burrowing bivalves such as *Asaphis dichotoma*, *Tellina palatum* and *Anodontia edentula* were commonly uncovered, particularly at Station 3.8, but living specimens could not be found.

The shingle ramparts, a feature peculiar to these islands, provide a further habitat for infaunal species in places where the interstices have become infilled and consolidated with finer sediment. On Three Isles (Station 3.11) excavation at the base of the rampart yielded a variety of polychaetes, chiefly *Perinereis cultrifera helleri*, syllid sp. and *D. caducus*, with *S. cumanense*, several alpheid spp. and the large ophiuroid *Macrophiothrix koehleri*.

The inland tidal pools on some low wooded islands, for example Nymph, Turtle II and West Pethebridge, present an interesting environment for further study. Here it is worthwhile recording that on Nymph I. (Station N2) a very localized population of *Mictyris* sp. affin. *livingstonei* (see McNeill 1926) exists along the banks of the outflow channel, together with *Uca* sp.

Associations

Although our knowledge of the relations between partners is generally rather scant, associations between animals are common on mud and sand flats in many areas of the world, and the wide variety of associations to be found in localities within the Indo-West Pacific region is well exemplified by those described from Inhaca Island, Mozambique (see Macnae & Kalk 1962). Similar, but less well documented, examples occur in Queensland waters, and during the course of the present investigations of the sand flat fauna a number of associations were discovered, mostly instances of commensalism, that is, of a type where the partnership appears to be advantageous to one member without the other being inconvenienced or harmed (Dales 1957). These associations and their occurrences are summarized in table 2.

Description of plate 2

Figure 7. A dense aggregation of the chaetopterid polychaete *Mesochaetopterus sagittarius sagittarius*. Scale is 5.5 cm in diameter. Ingram Island, Station IN1, 22 October.

Figure 8. A specimen of the spatangoid *Maretia planulata* emerging at the sand surface at low water mark in the late afternoon just before immersion by the incoming tide. Low Isles, Station L5, 26 August.

Figure 9. Three specimens (5.1–7.8 mm in length) of the commensal bivalve '*Erycina*' sp. 2 attached to the posterior end of the trunk of *Sipunculus robustus*. Three Isles, Station 3.6, 13 September.

Figure 10. Three specimens (1.3–5.4 mm in length) of the commensal bivalve '*Erycina*' sp. 3 attached to the dorsal side of *Fimbria fimbriata* (78.0 mm in length). Two Isles, Station 2.4, 22 September.

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One of the most common and widespread of associations in the western Pacific is that of the polynoid *Gastrolepidia clavigera* living on holothurians (see Gibbs 1969, 1971). Although largely unrecorded in the Great Barrier Reef region (but see Whitley & Boardman 1929), this polychaete is associated with at least six holothurian species (Gibbs, Clark & Clark 1976) and on the sand flats individuals of *Stichopus chloronotus* and *Holothuria atra* often harbour this commensal. On Two Is and Three Is between 2 and 6 % of *H. atra* and between 6 and 40 % of *S. chloronotus* were found to have one or two *Gastrolepidia* clinging to their undersurfaces.

Table 2. List of commensal species and their hosts found on sand flats within the survey area

Abbreviations: As, Asteroidea; De, Decapoda; En, Enteropneusta; Ho, Holothurioidea; La, Lamellibranchia; Pi, Pisces; Po, Polychaeta; Si, Sipuncula; St, Stomatopoda.

host		commensal		station
Chaetopterus variopedatus	(Po)	*Tetrias* sp. aff. *fischeri*	(De)	L6
Loimia medusa	(Po)	*Ophiodromus* sp. cf. *berrisfordi*	(Po)	L6
Paraspidosiphon klunzingeri	(Si)	'*Erycina*' sp. 1	(La)	IN1
Siphonosoma cumanense	(Si)	*Fronsella* sp.	(La)	L5 IN2
Sipunculus robustus	(Si)	'*Erycina*' sp. 2	(La)	L2 3.6
Lysiosquilla maculata	(St)	'*Devonia*' sp.	(La)	L5
		'*Galeomma*' sp	(La)	L3 L5
		Phlyctaenachlamys lysiosquillina	(La)	L2 L3 L5
?*Pinna muricata*	(La)	*Pinnotheres* sp.	(De)	L7
Fimbria fimbriata	(La)	'*Erycina*' sp. 3	(La)	L5 L6 L7 2.4 IN2
Archaster typicus	(As)	*Ophiodromus* sp.	(Po)	Hampton
Chiridota rigida	(Ho)	'Leptonid' sp.	(La)	L3
Holothuria arenicola	(Ho)	*Carapus homei*	(Pi)	L4
Holothuria atra	(Ho)	*Gastrolepidia clavigera*	(Po)	gen
Labidodemas semperianum	(Ho)	*Porcellana* sp.	(De)	L3
Stichopus chloronotus	(Ho)	*Gastrolepidia clavigera*	(Po)	gen
Balanoglossus australiensis	(En)	*Ophiodromus* sp. cf. *berrisfordi*	(Po)	gen
Balanoglossus carnosus	(En)	*Lepidasthenia* sp. cf. *terrareginae*	(Po)	L2
Balanoglossus studiosorum	(En)	*Ophiodromus* sp. cf. *berrisfordi*	(Po)	Turtle I

The abundance of enteropneusts on the sand flats has been referred to above, and it is not surprising that several commensals are to be found living in their burrows. The commonest of these is the hesionid polychaete *Ophiodromus*, which typically lives singly with *Balanoglossus australiensis*. This *Ophiodromus* sp. is deep brown in colour and thus is rather conspicuous on its dull yellow host. It is an active species and readily leaves the enteropneust when disturbed, a fact which may account for this polychaete being overlooked in the past. In some areas, for example at Station L3, 40–50 % of the *B. australiensis* population shelter this commensal. *Ophiodromus* was found on one occasion with *B. studiosorum* (on Turtle I), but is not confined to enteropneusts since it was also found cohabiting a tube of the terebellid *Loimia medusa*. The species is close to *O. berrisfordi* Day, but is probably new. A second *Ophiodromus* sp. inhabits the ambulacral groove of *Archaster typicus* (one example from Hampton I).

Another polychaete commensal of enteropneusts is the polynoid *Lepidasthenia*. In this case, only a single specimen was discovered living in the burrow of a *B. carnosus*. Although close to *L. terrareginae* (also described from Low Isles by Monro (1931)), the specimen appears to belong to an undescribed species.

Commensal crabs include the pinnotherid *Tetrias* sp. (affin. *fischeri*) and *Porcellana* sp. (nr *ornata*). A pair of the former (male and female) were cohabiting a tube of the polychaete

Chaetopterus variopedatus and one individual of the latter was found in the burrow of the holothurian *Labidodemas semperianum* clinging to the body of its host. A single specimen of a *Pinnotheres* sp. (female) was also retrieved from a collection of molluscs from the Low Isles sand flat which included a specimen of *Pinna muricata*, its probable host.

As a group, commensal bivalves belonging to the superfamily Galeommatacea are well represented in the present collections: a total of 30 specimens comprising eight species were taken, several of which will probably require description as new species. The taxonomy of this group requires revision and the names used here, kindly provided by Dr W. F. Ponder, are provisional. Of particular interest are those forms which utilize the burrows of the large stomatopod *Lysiosquilla maculata*, attaching themselves to the mud lining of the burrow, usually within a distance of about 15 cm of the entrance. Although many *Lysiosquilla* burrows were excavated throughout the survey area, curiously, commensal bivalves were detected in only three, all at stations on the Low Isles sand flat, in the following numbers:

Species	Station		
	L2	L3	L5
Phlyctaenachlamys lysiosquillina	1	3	1
'*Galeomma*' sp.	—	2	2
'*Devonia*' sp.	—	—	1

As shown, at least three species are present and all may be living in the same burrow. The best known of these species is *P. lysiosquillina*, described by Popham (1939) from material collected by the 1928–29 Expedition on Low Isles. However, it does not appear to have been subsequently found elsewhere, although the host is widely distributed in the Indo-Pacific region. '*Galeomma*' sp. is of similar overall size to *P. lysiosquillina* with a shell length of 4–8 mm; in the field, its all-white mantle readily distinguishes it from *P. lysiosquillina*, which has orange coloured mantle papillae and tentacles. The third species, '*Devonia*', is represented by a single specimen 4.6 mm long.

Such commensal bivalves do not appear to frequent the 'vestibules' of *Axius* burrows which, although smaller, appear to present a similar niche as offered by the *Lysiosquilla* burrows. However, a more effective method of investigation other than excavation by digging might reveal bivalves inhabiting the deeper parts of the burrow system (cf. Farrow 1971). Elsewhere in Australian waters, *Axius* burrows harbour a number of bivalve species (see Cotton 1938).

Relatively few associations between bivalves and sipunculans have been recorded (see Stephen & Edmonds 1972), and thus it is perhaps surprising that associations involving three bivalves and three sipunculan species should be represented. Three individuals of the large sipunculan *Sipunculus robustus* were discovered with specimens of '*Erycina*' sp. 2, 5–10 mm in length, attached by byssus threads to the posterior end of the trunk. Two of these sipunculans had single commensals but the third had three (figure 9, plate 2). The latter was taken from a shallow burrow, about 1.0 cm below the sand surface beneath a beach-rock boulder (Station 3.6). A similar but unnamed bivalve living commensally on *S. robustus* is known from the Palau Islands (Satô 1935) and Banda Neira (Wesenberg-Lund 1954). Another species of '*Erycina*' (sp. 1) and *Fronsella* sp. occurred singly, attached to their respective hosts *P. klunzingeri* (one example) and *S. cumanense* (two examples); both of these bivalves are small, 2.5–3.2 mm in length. A further bivalve is of similar habit, namely 'Leptonid' sp., and this lives commensally on the holothurian *Chiridota rigida*, resembling *Devonia* spp. on synaptids (Anthony 1916; Ohshima 1930, 1931).

The association between the two bivalves '*Erycina*' sp. 3 and *Fimbria fimbriata* is of interest because of its frequency of occurrence in the survey area. Only eight specimens of the conspicuous white, surface-burrowing host were found, but five of these each had two or (in one case) three individuals of the '*Erycina*' sp. attached by byssus threads on the dorsal side to the posterior of the hinge line (figure 10, plate 2). The smallest of these '*Erycina*' is only 1.3 mm, the largest 5.4 mm in length.

The list of associations found on the sand flats is completed in mentioning *Carapus homei*, a well known associate of echinoderms (Mukerji 1932; Jangoux 1974) a specimen of which revealed itself in escaping from the cloaca of a *Holothuria arenicola* dug up on Low Isles.

Discussion

The zonation of the fauna on the sloping beaches of the sand cays of low wooded islands is similar to that found in other Indo–West Pacific regions. As typical for most tropical sandy shores, *Ocypode* is dominant at high water level (see, for example, Dahl 1953; Hartnoll 1975) with the two widespread species *O. ceratophthalma* and *O. cordimana* generally occurring in mixed populations. The record of *O. kuhli* de Haan from Low Isles is considered doubtful and requiring verification (McNeill 1968). Between mid-tide level and low water neaps, mesodesmatid beds are a common entity and similar aggregations of *Atactodea* and *Davila* are widespread in the lagoon environments of Indo-Pacific atolls (Banner 1952; Cloud 1952; Beu 1972). In northern Queensland the same zone is often occupied by several hippid species, mainly *H. celaeno*; although feeding was not observed, these mole-crabs presumably perform a scavenging rôle in the same manner as described for related forms (see Mortensen 1922; Bonnet 1946; Matthews 1955).

Over the sand flat, bivalves are scarce and the surface-burrowing forms are mainly gastropods, many of which are widely distributed species found throughout the Indo–Pacific (cf. Morrison 1954; Taylor 1971; Gibbs 1975). The infauna, while consisting of numerous species, tends to be dominated numerically by relatively few forms with *Edwardsia*, chaetopterids, other tubicolous polychaetes and *Balanoglossus* spp. forming the bulk of the macrofauna. As a group, the polychaetes have been largely neglected in past surveys in the area; for example, less than 10 species were recorded for the Low Isles sand flat by the 1928–29 and 1954 Expeditions, whereas over 30 species were taken in 1973. In all, over 50 species occur on the sand flats, a high proportion of which, although Indo-Pacific in distribution, are here recorded for the first time for the Province as a whole. The burrowing echinoderms are equally interesting, particularly on Low Isles where four spatangoids, one clypeastroid, two ophiuroids and four or five holothurians exist. The specimens of *Amphioplus bocki* are the first recorded from Australian waters while *Amphiura diacritica* and *Leptosynapta latipatina* were previously known only from the holotypes collected respectively in the Whitsunday Group (Clark 1938) and at Friday Island (Clark 1921, 1946). *Maretia planulata* seems to have been absent from the Low Isles sand flat in 1928–29 but was common there in 1954 (Endean 1956). Since the species is frequently plentiful in sandy deposits in shallow depths, it is possible that the upper limit of the Anchorage population may fluctuate according to conditions at the level of low water.

An assessment of the changes which have occurred in the species composition and relative abundance of the Low Isles sand flat fauna between 1928–29, 1954 and 1973 proves difficult for several reasons (see Stoddart, McLean, Scoffin & Gibbs 1978, this volume) but chiefly

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because the earlier studies of this habitat were brief and the ecological data are rather fragmentary. However, in terms of the dominant species, *Edwardsia*, *Mesochaetopterus* and *Balanoglossus* remain abundant while such species as *Aspidosiphon cumingi* and *Phyllodoce malmgreni*, reported as plentiful in 1928, could not be found in 1973. Conversely, quite a number of the more conspicuous tubicolous polychaetes taken in 1973, including *Phyllochaetopterus*, *Spiochaetopterus*, *Loimia* and *Sabella*, do not appear in the 1928–29 reports (Monro 1931). In view of the present-day abundance of chaetopterids, the statement in Stephenson *et al.* (1931, p. 73) that 'the polychaetes as a whole do not appear to be among the dominant groups, except in rocky crevices . . .' is difficult to interpret.

TABLE 3. SPECIES DIVERSITY OF THE SAND FLAT FAUNA ON LOW ISLES AND OTHER ISLANDS IN THE SURVEY AREA

	number of species		
group	Low Isles	other islands	total
Anthozoa	2	3	3
Polychaeta	30+	44+	50+
Sipuncula	5	4	6
Echiura	—	1	1
Crustacea	*ca.* 10	*ca.* 15	*ca.* 20
Gastropoda	24	26	36
Lamellibranchia	13	11	17
Echinodermata	16	8	17
Enteropneusta	3	3	3
total	**103**	**115**	**153**

Attention can also be focused on the anomuran *Axius* (*Neaxius*) sp., a fairly common and conspicuous animal in the survey area but one which is not mentioned in earlier accounts (see McNeill 1968). Possibly its burrows were misidentified as being constructed by small *Lysiosquilla*. The species may be very localized in its distribution since the genus *Axius* appears to have been recorded in the province only once (Port Molle), the single specimen being uncertainly referred to *Axius* (*Neaxius*) *plectrorhynchus* Strahl by Miers (1884) (see also Fulton & Grant 1902).

The species diversity of the fauna of the sand flats in the survey area is summarized in table 3. Based on the present collections, the macrofauna can be estimated at 150–160 species although undoubtedly this total could be substantially increased with further study of past collections. However, the figures illustrate the importance of Low Isles as a locality for further investigation, in that about two-thirds of the species in the total sand flat fauna of the area are recorded from there and about one-fifth of all species were taken only on Low Isles, notably some little-known echinoderms. Further, it can be noted that of the 19 commensal associations discovered during the survey, no less than 16 were found on Low Isles.

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Gastropoda and Galeommatidae); Mrs S. Slack-Smith, Western Australian Museum Lamellibranchia, excluding Galeommatidae); Dr R. W. Ingle, British Museum (Natural History) (Crustacea); Miss A. M. Clark, Mrs C. M. Clark, British Museum (Natural History) (Echinodermata); Professor C. Burdon-Jones, James Cook University (Enteropneusta); Dr A. Wheeler, British Museum (Natural History) (Pisces). I am most grateful also to the Council of the Marine Biological Association of the U.K. and the Natural Environment Research Council for leave of absence during the period of the Expedition.

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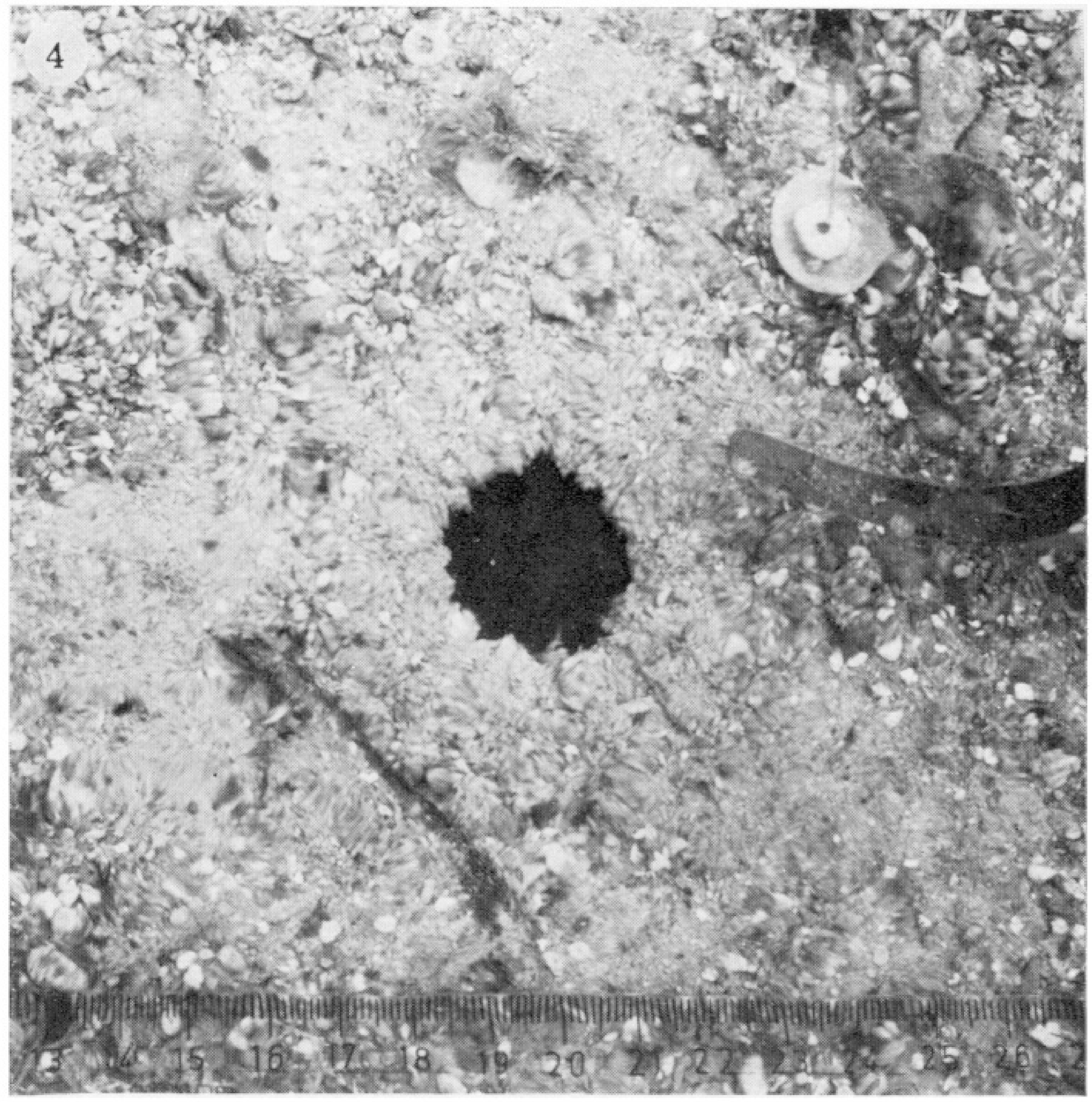


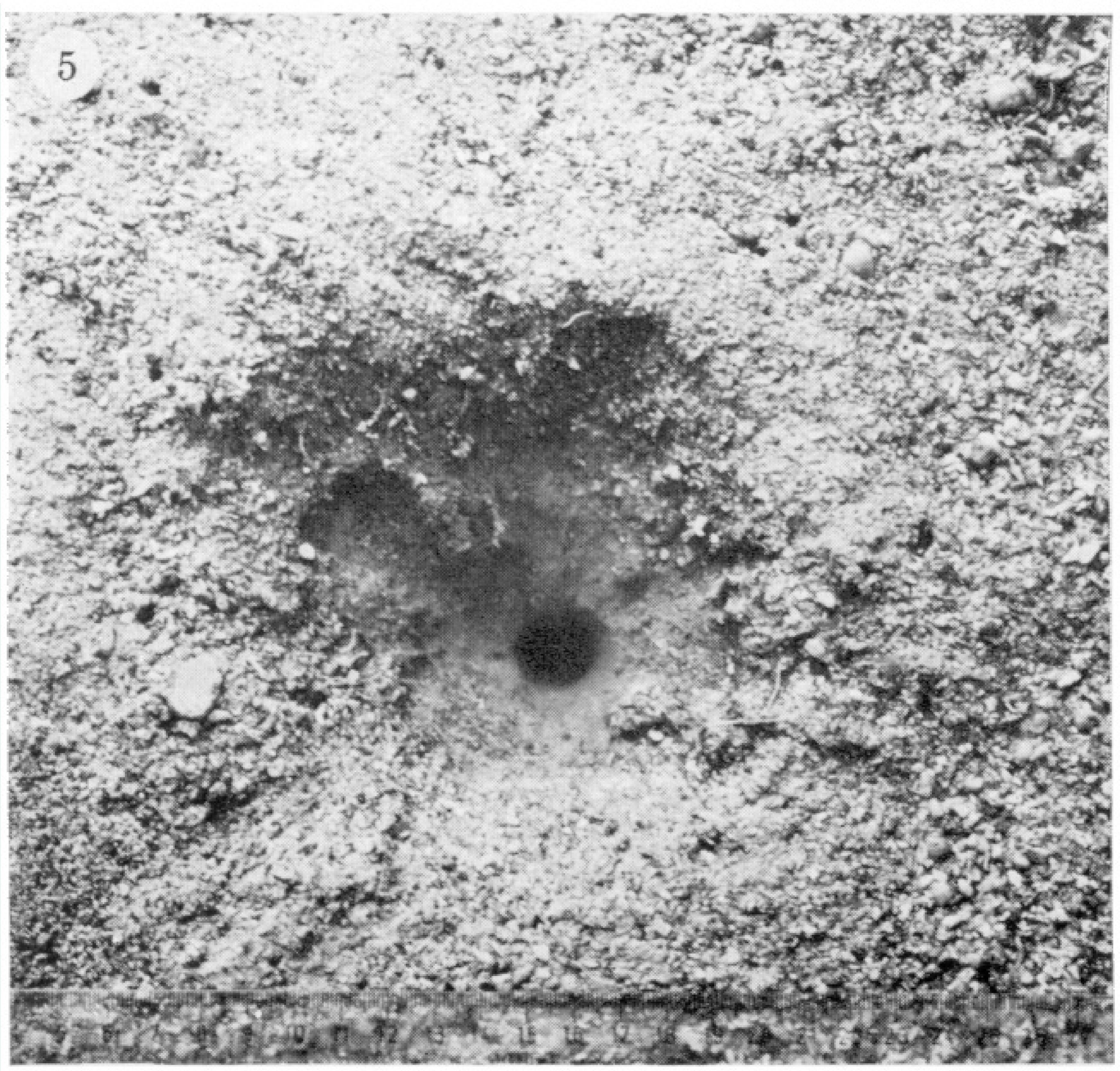
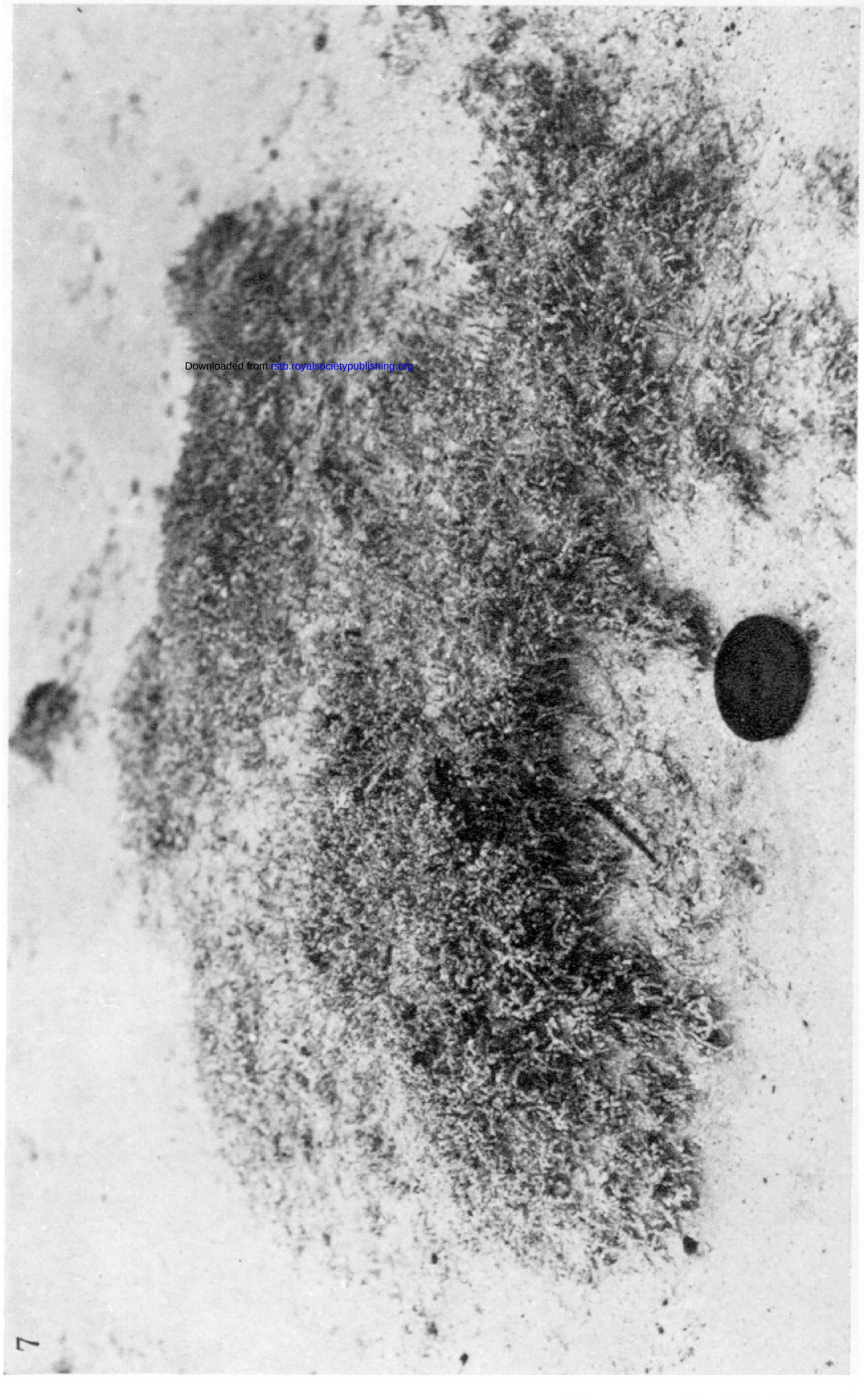


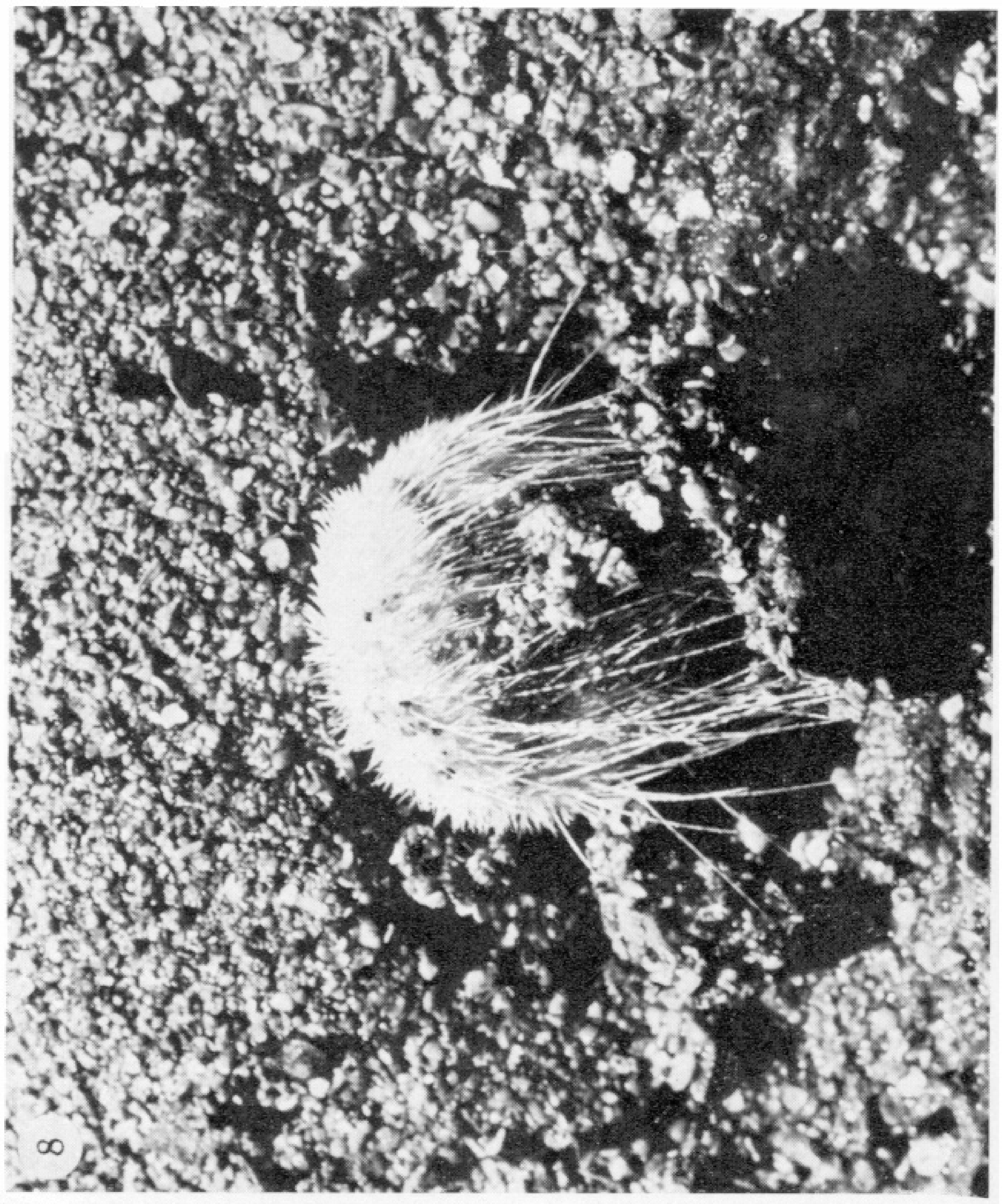
FIGURE 3. The faecal casts of the enteropneust *Balanoglossus carnosus* on the sand surface at low tide. Scale = 30 cm. Low Isles, Station L1, 27 August.

FIGURE 4. The entrance to the burrow of the stomatopod *Lysiosquilla maculata*. Low Isles, Station L1, 27 August.

FIGURE 5. The entrance to the burrow of *Axius* (*Neaxius*) sp. Low Isles, Station L1, 27 August.

FIGURE 6. The entrance to the burrow of ? alpheid sp. Low Isles, Station L2, 27 August.





FIGURES 7–10. For description see opposite.