405

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Marine Flora and Fauna of the Northeastern United States. Echinodermata: Holothuroidea

David L. Pawson

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Juanita M. Kreps, Secretary

National Oceanic and Atmospheric Administration

Richard A. Frank, Administrator

National Marine Fisheries Service

Robert W. Schoning, Director

FOREWORD

This issue of the "Circulars" is part of a subseries entitled "Marine Flora and Fauna of the Northeastern United States." This subseries will consist of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the northeastern United States. Manuals will be published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith, published in 1964, and produced under the auspices of the Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass. Instead of revising the "Woods Hole Keys," the staff of the Systematics-Ecology Program decided to expand the geographic coverage and bathymetric range and produce the keys in an entirely new set of expanded publications.

The "Marine Flora and Fauna of the Northeastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual will be based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each major taxon, treated in a separate manual, will include an introduction, illustrated glossary, uniform originally illustrated keys, annotated check list with information when available on distribution, habitat, life history, and related biology, references to the major literature of the group, and a systematic index.

These manuals are intended for use by biology students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. In many instances the manuals will serve as a guide to additional information about the species or the group.

Geographic coverage of the "Marine Flora and Fauna of the Northeastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200-m depth on the continental shelf from Maine to Virginia, but may vary somewhat with each major taxon and the interests of collaborators. Whenever possible representative specimens dealt with in the manuals will be deposited in the reference collections of major museums in the region.

After a sufficient number of manuals of related taxonomic groups have been published, the manuals will be revised, grouped, and issued as special volumes. These volumes will thus consist of compilations of individual manuals within phyla such as the Cnidaria, Arthropoda, and Mollusca, or of groups of phyla.

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Marine Flora and Fauna of the Northeastern United States. Echinodermata: Holothuroidea

DAVID L. PAWSON¹

ABSTRACT

The holothurian fauna of the east coast of the United States from southern New Jersey to Nova Scotia, to depths of 200 m, comprises 21 species in 17 genera and 8 families. An introduction to the general biology and morphology of the holothurians, systematic characters and examination procedures, and a selected bibliography are included, together with an illustrated key to the species, an annotated systematic list, and an index. Affinities of this fauna are chiefly boreal; some species also occur south of Cape Hatteras, while others are essentially Arctic in distribution.

INTRODUCTION

Holothurians or sea cucumbers are usually inconspicuous, soft-bodied animals, often unattractive in appearance, which at first glance seem to belie their close relationship with the more aesthetically pleasing sea stars and sea urchins. But closer examination reveals the five-part (pentamerous) symmetry that is typical of living echinoderms, although in the holothurians the pentamery is often obscured by a more or less conspicuous bilateral symmetry. A skeleton of calcium carbonate in the form of calcite is present, though the elements are usually reduced to microscopic ossicles (see Hyman 1955 and Boolootian 1966).

In the tropics, large aspidochirotid species 30 cm or more in length are very common, and the holothurians are a conspicuous element in shallow-water faunas, but in the temperate waters of the northeastern United States most are secretive, living buried in sand or mud, or concealed under rocks. A single relatively large species, *Cucumaria frondosa* (Gunnerus), is common on rocks along the coast of Maine, just below lowtide level (Jordan 1972). Some species are, however, important members of offshore benthic communities, and can reach population densities of many hundreds of individuals per square meter. They are efficient reworkers of seafloor sediments (for example, see Rhoads and Young 1971), and in many areas of the deep sea can comprise more than 90% of the total biomass present (Zenkevitch 1963).

With few exceptions, holothurians are sedentary; some, such as the psolids, may remain fixed to the same spot for years at a time. Dispersal is effected by transport of larval stages in currents to other localities. Some have planktotrophic larvae; others have yolky ciliated vitellaria larvae. Commonly, populations of a species may die off in an area and remain absent for a considerable number of years, until the area is repopulated by a new settlement of larvae.

Affinities of the northeastern United States holothurians are chiefly boreal; several of the species also occur around Europe and in the Arctic. Some species extend southward below Cape Hatteras, even into the Caribbean. Others are known only from the northeastern United States and Canadian coasts (Clark 1901; Coe 1912).

The fauna lacks representatives of the Order Aspidochirotida. The large *Parastichopus californicus* (Stimpson), so typical of the northwestern United States' shallow waters, has no counterpart on the east coast. The Order Dendrochirotida is well represented and at least one species, *Sclerodactyla briareus* (Lesueur), is a commonly used experimental animal (Farmanfarmanian 1969, Ellington 1976).

The 21 species dealt with here occur in depths of 200 m or less off the northeastern United States; a small number of forms of doubtful status were omitted. Only those species recorded from the area bordered to the south by southern New Jersey and to the north by Nova Scotia, Canada, were included.

Literature on holothurians of the northwest Atlantic is scanty. Very little information is available on ecology, physiology, and other aspects of the biology of most species. The best systematic study of the fauna is that of Deichmann (1930), which remains the standard work, although some of the nomenclature is now outdated.

The key provided here includes illustrations of important taxonomic characters. Most species are illustrated, and where desirable in the key, illustrations of ossicles or other anatomical features are included.

MORPHOLOGY

Figures 1 and 2 show basic features of the external and internal morphology of a holothurian. Holothurians generally tend to be cylindrical, with mouth and anus at opposite ends of the body. The mouth is surrounded by 10 or more tentacles. Typically there are five rows of suckorial tube feet, which form radii, the radii running from the anterior end of the body to the posterior end. Three

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Figure 1.—External features of a holothurian, viewed from the ventral side.

radii are ventral and two are dorsal; spaces between the radii are termed interradii.

The dermal layer of the body wall contains numerous microscopic calcareous ossicles (often termed calcareous deposits or spicules), which assume a great variety of shapes and which are very useful in classification.

The extensive coelomic cavity is lined with circular muscles, and five conspicuous longitudinal muscles define the radii. The mouth opens into an esophagus, which leads to a stomach (often poorly differentiated) and intestine. The intestine describes a large loop, then

runs to the terminal anus via the rectum. Two branching respiratory trees may arise from the rectum and extend anteriorly in the coelom; these are used in respiration and excretion of waste materials. A ring of calcareous plates, the calcareous ring, surrounds the esophagus, and this serves as the point of attachment for the retractor muscles, which serve to withdraw the anterior end of the body (the introvert) into the coelomic cavity when the animal contracts.

A part of the coelom forms the water vascular system, which is a system of fluid-filled vessels used in feeding, locomotion, and respiration. A ring vessel immediately posterior to the calcareous ring carries a stone canal in the middorsal interradius, the stone canal terminating in an internal madreporite. A polian vesicle arises from the ventral side of the ring vessel and hangs into the coelom. From the ring vessel five radial water vessels run anteriorly, giving rise to vessels serving the tentacles, and then posteriorly in the radii, giving rise to the tube feet, which penetrate the body wall to the exterior.

The sexes are separate. The gonad comprises one or two bunches of caeca hanging free in the body cavity. A genital duct arises from the confluence of the caeca and runs anteriorly in the dorsal mesentery to open to the exterior in the middorsal interradius near the tentacles.

Figure 2.—Internal features of a cucumariid holothurian, dissected from the left side.

SYSTEMATIC CHARACTERS

External Characters

Shape is highly variable. Some species are U-shaped, others cylindrical or even wormlike. A conspicuous tail may be present. The tube feet may be restricted to the radii in well defined rows, or they may be scattered all over the radii and interradii in various characteristic patterns. The Orders Apodida and Molpadiida lack tube feet. Tentacles may be dendritic, digitate, or pinnate. There are usually 10 tentacles, but some groups have 15-30, and many apodous species have 12 or 13.

Internal Characters

The calcareous ring is of particular importance (Pawson and Fell 1965). The ring may have well developed posterior projections, moderately developed projections, or none at all. The ring itself is typically composed of 10 pieces, but many apodous species have 12, and in some forms the ring is composed of a mosaic of numerous pieces. Other features of the water vascular system and musculature are useful in classification, but are not relevant to the species being considered here.

Ossicles

These are found in the body wall, tentacles, and tube feet, and they display a bewildering variety of shapes and sizes. They are of paramount importance in classification, particularly at the level of the genus and species. Certain types of ossicles have convenient names, such as buttons, plates, tables, wheels, anchors (see Fig. 3), and the various major groups of holothurians have characteristic types of ossicles. In the Order Dendrochirotida smooth or knobbed plates are common; small plates are often termed buttons. Baskets or cups occur frequently, and some taxa have tables, which consist of a flat perforated disk surmounted by a spire composed of two or more columns joined at their distal extremity. Rods occur in the tube feet and tentacles. Members of the Order

Figure 3.—Some typical holothurian ossicles: A. knobbed button; B. shallow cup; C. plate; D. rod; E. smooth button; F. wheel; G. anchor plate; H. anchor. A-E. Dendrochirotida; F. Apodida, Chiridotidae; G, H. Apodida, Synaptidae.

Apodida may have either anchors and anchor plates (Family Synaptidae) or wheels (Families Chiridotidae and Myriotrochidae) (see Clark 1924). Rods of various types may also be present. In the Order Molpadiida the ossicles can take the form of tables, and sometimes characteristic anchors and plates are present. In many molpadiids the ossicles are transformed into wine-red "phosphatic deposits" as the animal grows; these give the body wall a distinctive light to dark red color.

EXAMINATION PROCEDURES

Holothurians generally contract when preserved, withdrawing their tentacles, and changing their shape dramatically. They can be effectively narcotized with Epsom salts (MgSO_4) in seawater before fixation. Specimens should be preserved in 70% ethyl alcohol; acid conditions in formaldehyde tend to dissolve the ossicles with passage of time.

Dissection is best effected by making a longitudinal incision along the left or right side of the body. Most organs are easily seen when the body cavity is opened in this way.

Ossicles are usually smaller than 1 mm in diameter (many are $50\ \mu\text{m}$ or less) and must be examined with a compound microscope. They can be extracted by immersion of a small piece of the body wall in household bleach solution, or in sodium hypochlorite. The soft tissues are dissolved away, leaving the ossicles. Usually, body wall samples from the middorsal area will reveal typical ossicles. Permanent microscope slides can be made by washing the ossicles several times in distilled water, and mounting them in Canada balsam or some other permanent medium.

GLOSSARY

Aspidochirotida An Order of Holothuroidea which includes forms with shield-shaped tentacles and a thick body wall. Comprises mostly tropical and deep-sea species.

calcareous ring A ring of solid plates of calcite surrounding and supporting the esophagus and related structures.

dendritic Branching profusely.

Dendrochirotida An Order of Holothuroidea which includes forms with richly branching tentacles.

digitate Possessing fingerlike projections.

genital duct A tube which links the gonad to the exterior and carries eggs or sperm into the surrounding seawater.

introvert In Dendrochirotida, the anterior part of the body, comprising tentacles, calcareous ring and related structures, which can be retracted by contraction of retractor muscles.

madreporite A sievelike plate through which water may be drawn into the water-vascular system. Internal in most shallow-water holothurians, external in many deep-sea forms.

ossicles Usually small, distinctively shaped, skeletal elements composed of calcium carbonate in form of calcite.

pentamerous Having five-part symmetry.

pinnate Featherlike. Used for tentacles with numerous digits.

planktotrophic Able to feed on planktonic organisms.

polian vesicle In water-vascular system, a contractile sac in which excess fluid may be stored.

psolids Dendrochirotid holothurians in which the upper surface of the body is covered with large overlapping ossicles, and the lower surface is in the form of a soft sole.

retractor muscles In dendrochirotids, set of five muscles used to retract the introvert.

ring vessel In water-vascular system, a vessel surround-

ing esophagus, which gives rise to polian vesicle, stone canal, and radial vessels.

sole In psolids, the soft ventral surface of the body.

stone canal In water-vascular system, a tube, often calcified, which links the madreporite to the ring vessel.

tentacles Dendritic, digitate, or shield-shaped anterior extensions of the water-vascular system which surround the mouth and are used in feeding.

tube feet Hollow extensions of water-vascular system which project through body wall. Locomotory organs; display great variety in number and arrangement.

vitellaria A type of larval stage richly supplied with yolk, upon which the larva feeds.

water-vascular system A system of fluid-filled vessels used in respiration, locomotion, nutrition, and sensory perception. On external surface of body manifested as tube feet and tentacles.

KEY TO HOLOTHURIANS OF THE NORTHEASTERN UNITED STATES INSHORE AND SHELF WATERS

- 1 Body with typical tube feet, which may be scattered or restricted to well-defined areas (radii). Ten or 20 tentacles, richly branched (dendritic). Body wall generally firm, leathery 2

- 1 Body totally lacking tube feet. Twelve or 15 tentacles, with fingerlike branches (digitate or pinnate). Body wall leathery and opaque or fragile and translucent 15

- 2 (1) Body generally cylindrical, often tapering anteriorly and posteriorly, never partly enclosed in a test of conspicuously overlapping scales 3

- 2 (1) Body with flattened ventral surface; dorsal surface arched, covered by a test of overlapping scales. Ventral surface (sole) soft, with tube feet around edge and sometimes along midventral radius 14

- 3 (2) Calcareous ring with no posterior projections; posterior margin of ring undulating. Tentacles 10 or 20. Tube feet scattered over body wall or tending to be confined to radii 4

- 3 (2) Calcareous ring with long (a) or short (b) posterior projections. Tentacles 10. Tube feet confined to radii or scattered over body wall 11

- 4 (3) Tentacles 20, 10 large and 10 small, arranged in 2 rings. Ossicles tables, which tend to disappear with age 5

- 4 (3) Tentacles 10, of which 2 ventral ones are smaller than others. No tables 6

- 5 (4) Tube feet tend to be scattered uniformly over body. Ossicles robust tables with low spire ending in numerous teeth. Body wall thin, translucent. Maximum size 15 cm, color whitish or brownish
 Thyonidium pellucidum

- 5 (4) Tube feet tend to be aggregated in radii and scattered in interradii. Ossicles delicate tables with high spire ending in few teeth. Body wall thick, not translucent. Maximum size 10-15 cm, color whitish or yellowish
 Duasmodactyla commune

- 6 (4) Tube feet uniformly scattered over radii and interradii. Calcareous ring with undulating posterior edge or with rudimentary projections. Ossicles buttons (a) and cups (b). Maximum size 7 cm, color whitish with brown spots, or uniform pale brown*Thyonella pervicax*

- 6 (4) Tube feet tend to be aggregated along radii, especially ventrally, but may also be present, scattered, in interradii 7

- 7 (6) Ossicles include numerous buttons and numerous cups, the latter rudimentary or with perforations 8

- 7 (6) Ossicles may include plates or buttons. No cups 10

- 8 (7) Feet absent from interradii. Ossicles knobbed buttons (a) and rudimentary cups (b) lacking perforations. Maximum size 2 cm, color light orange to white*Ocnus diomedea*

- 8 (7) Feet present in interradii, at least dorsally. Ossicles smooth or knobbed buttons and perforated flat cups 9

- 9 (8) Feet numerous, scattered in all interradia. Ossicles knobbed buttons (a) and cups (b). Maximum size 15 cm, color mottled brown
 Thyonella gemmata

- 9 (8) Feet very few, scattered in dorsal interradia only. Ossicles smooth buttons (a) and cups (b). Maximum size 1.5 cm, color white
 Trachythone nina

- 10 (7) Ossicles plates, which disappear as the animal grows. Tube feet generally restricted to radii, but also scattered dorsally. Maximum size 50 cm, color brown . . . *Cucumaria frondosa*

- 10 (7) Ossicles four-holed buttons with smooth to knobbed surface. Tube feet in double row in midventral radius, scattered elsewhere on body wall. Maximum size 5 cm, color white or pale tan to brown
 Stereoderma unisemita

- 11 (3) Posterior projections of calcareous ring short. Tube feet hairlike, scattered all over body wall. Ossicles tables with spire of four rods; tables few or often absent. Maximum size 10-12 cm, color brownish or greenish to nearly black *Sclerodactyla briareus*

- 11 (3) Posterior projections of calcareous ring very long. Tube feet scattered over body wall or restricted to radii. Ossicles include tables with spires usually composed of two rods (exceptionally 3-4 rods in *Pentamera calcigera*) 12

- 12 (11) Tube feet hairlike, scattered all over body wall. Ossicles very numerous tables (a). Maximum size 5-10 cm, color whitish to brownish *Havelockia scabra*

- 12 (11) Tube feet restricted to radii, in five distinct crowded bands. Ossicles tables and few to many plates 13

- 13 (12) Tables (a) variable in shape, overlying densely crowded layer of plates (b)., Maximum size 9 cm, color white *Pentamera calcigera*

- 13 (12) Tables (a) usually oval, with four holes; elongate plates occasionally found. Maximum size 5 cm, color white or dirty brown
 Pentamera pulcherrima

- 14 (2) Taillike projection present on posterior end of dorsal surface of body. On sole, midventral radius with complete double row of tube feet. Maximum size about 15 cm, largest specimens black, smaller specimens often yellowish-brown *Psolus phantapus*

- 14 (2) No taillike projection. On sole, midventral radius without complete double row of tube feet. Maximum size about 19 cm, color bright scarlet red or reddish-orange *Psolus fabricii*

- 15 (1) Plump, tapering posteriorly to form a well-defined tail. Body wall opaque, leathery. Fifteen digitate tentacles (a) 16

- 15 (1) Cylindrical and worm-like, with 12 pin-nate tentacles (a) and translucent body wall 17

- 16 (15) Color whitish. Ossicles include tables (a) with about 14 holes and a central spire. Maximum size 25 cm
..... *Caudina arenata*

- 16 (15) Color light red to very dark red or blackish. Ossicles in body replaced by wine-red phosphatic deposits as animal grows. Deposits in tail (a) unaffected. Maximum size 20 cm
..... *Molpadia oolitica*

17 (1) Ossicles as wheels, or as anchors with anchor plates 18

17 (1) Ossicles rods only; no wheels, anchors or anchor plates. Maximum size 4 cm, color red-brown
 Toxodora ferruginea

18 (17) Ossicles wheels, gathered into papillae 19

18 (17) Ossicles anchors (a) associated with anchor plates (b). 20

19 (18) In addition to wheel papillae, body wall contains numerous curved rods with bifurcated ends. Tentacles with 5-7 pairs of digits. Maximum size 12 cm, color dark reddish-brown .
 Chiridota wigleyi

19 (18) Curved rods absent. Tentacles with 2-3 pairs of digits. Maximum size 20 cm, color usually pinkish *Chiridota laevis*

- 20 (18) Tentacles with 4-6 pairs of digits. Radial pieces of calcareous ring (a) perforated for passage of radial nerve. Maximum size 15 cm, color generally whitish . . . *Leptosynapta tenuis*

- 20 (18) Tentacles with 2-4 pairs of digits. Radial pieces of calcareous ring (a) not perforated for radial nerve, but notched anteriorly. Maximum size 10 cm, color generally pinkish *Epitomapta roseola*

ANNOTATED SYSTEMATIC LIST

The species are arranged here according to currently accepted classifications (see Deichman 1930, Pawson and Fell 1965). Notes on distribution and habitat are included.

Class HOLOTHUROIDEA

Order Dendrochirotida

FAMILY PSOLIDAE

Psolus phantapus (Strussenfeldt 1765). Off coast of New England to Labrador; Greenland, Iceland, Great Britain, Scandinavia; 20-250 m. Lives attached to hard substrates on gravelly bottoms, or on surface of silty sand.

Psolus fabricii Duben and Koren 1846. Off Massachusetts and northwards to Ungava Bay, Greenland, Norway; intertidal (in north)—1800+ m.

FAMILY PHYLLOPHORIDAE

Pentamera pulcherrima Ayres 1854. Coast of New England to North Carolina; also Gulf coast of Texas and Colombia; shallow water. In North Carolina buried in mud. Occasionally washed ashore after storms in New England.

Pentamera calcigera (Stimpson 1851). New England coast to Labrador and northward, western Greenland, Alaska and Bering Sea; 10-100 m. Often found in sand, and frequently washed ashore after storms. Eaten by fish.

Havelockia scabra (Verrill 1873). Halifax, Nova Scotia, to Long Island; 10-1,170 m. Most common on sandy-silt bottoms.

FAMILY SCLERODACTYLIDAE

Sclerodactyla briareus (Lesueur 1824). Nova Scotia south along Atlantic coast to Gulf coast of Texas; 0-20 m. Often found in muddy localities, buried or associated with eelgrass. A widely used experimental animal, referred to formerly as *Thyone briareus*.

FAMILY CUCUMARIIDAE

Cucumaria frondosa (Gunnerus 1770). Nantucket, New England northward; Iceland, Greenland, northern Europe; 0-260 m. Commonly found clinging to rocks below low water mark; also occurs on sand.

Trachythyone nina (Deichmann 1930). East of Cape Cod; 190-250 m. On gravel and shell-sand bottoms.

Stereoderma unisemita (Stimpson 1851). Newfoundland to Long Island Sound; 10-200 m. Sand or gravel bottom.

Ocnus diomedae Pawson 1976. East of Cape Cod; 190-250 m. Gravel bottoms.

Thyonidium pellucidum Duben and Koren 1844. Casco Bay, Maine, to Labrador, Newfoundland, Iceland, Greenland, Great Britain, Scandinavia; 40-120 m. Gravelly or shelly bottom.

Duasmodyctyla commune (Forbes 1841). Coast of New England and Newfoundland; northern Europe; 0-190 m. Commonly found under stones or buried in gravel near low water mark.

Thyonella gemmata (Pourtales 1851). Woods Hole, Mass., to Yucatan; shallow water. Common in Gulf of Mexico. Buried in mud or sand; frequently washed ashore in large numbers.

Thyonella pervicax (Theel 1886). Vineyard Sound, Mass., to Gulf of Mexico and Brazil; shallow water.

Order Molpadiida

FAMILY MOLPADIIDAE

Molpadia oolitica (Pourtales 1851). From Newfoundland to New England; possibly extending to Florida; Bering Sea; 10-720 m. Partially buried in muddy substrates.

FAMILY CAUDINIDAE

Caudina arenata (Gould 1841). New Brunswick and coast of New England; 0-2,500 m. Buried in sand or mud, often washed ashore in great numbers after storms. Anatomy of this species studied by Gerould (1896).

Order Apodida

FAMILY SYNAPTIDAE

Leptosynapta tenuis (Ayres 1851). Coast of New England; Bermuda (?); shallow water. Usually buried near low water mark in sand or mud.

Epitomapta roseola (Verrill 1874). Massachusetts and Connecticut coasts; Bermuda; shallow water. Buried in sand or mud near low water mark, or under stones.

FAMILY CHIRIDOTIDAE

Chiridota laevis (Fabricius 1780). Massachusetts northward to Labrador and Greenland (exact range not known); 0-100 m. In sandy to muddy areas, often also among stones and seaweed.

Chiridota wigleyi Pawson 1976. East of Long Island, N.Y.; 90 m. Silty sand.

Toxodora ferruginea Verrill 1882. South of Nantucket and Martha's Vineyard; 140-280 m.

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COORDINATING EDITOR'S COMMENTS

Publication of the "Marine Flora and Fauna of the Northeastern United States" is most timely in view of the growing universal emphasis on environmental work and the urgent need for more precise and complete identification of coastal organisms than has been available. It is mandatory, wherever possible, that organisms be identified accurately to species. Accurate scientific names unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been inadequately studied.

David L. Pawson commenced his study of the systematics and zoogeography of echinoderms in 1958, working mainly on echinoids and holothuroids of the southern Pacific Ocean. In 1964 he joined the staff of the National Museum of Natural His-

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