

THE GENUS *HARPA* (MOLLUSCA:GASTROPODA) IN THE NEW WORLD

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I. ABSTRACT

The name *Harpa americana* has been applied to every fossil *Harpa* specimen found in the New World. A second example of true *H. americana* from the Gurabo Formation, Dominican Republic, shows that none should be so referred and the form that occurs in the Agueguexquite Formation of Mexico is here named *H. isthmica*, n. sp. The examples taken from the Esmeraldas Formation of Ecuador are better referred to the living West Coast species *H. crenata*.

II. INTRODUCTION

The gastropod genus *Harpa* is a good example of the group Woodring termed "paciphiles," that is, present in the Tertiary of the Caribbean but now extinct there while still living on the eastern Pacific coast (see Woodring, 1966, p. 428, table 1). Until recently the entire known occurrence of the genus in the fossil record of the New World consisted of only two specimens: the types of *H. myrmia* Olsson, 1931, from the Oligocene of Peru; and *H. americana* Pilsbry, 1922, from the "Miocene" of Santo Domingo.

There are also in the New World several Eocene species assigned to *Eocithara* Fischer, 1883, once considered as a subgenus of *Harpa* but now recognized as an extinct genus. Rehder (1973) has summarized all of the harpid species, both fossil and Recent, of the entire world (not a formidable task, for there are fewer than 50 species total) and concluded that *Eocithara*, with 16 species-groups, is known from beds of Upper Paleocene to Middle Miocene age and geographically from Pakistan to Europe and in North America from Mississippi to California.

The genus *Harpa* s.s., which is distinguished by its larger size, multispiral conical protoconch, and expanded parietal callus, was considered by Rehder to include eleven living and five fossil species. Nine of the living forms are Indo-Pacific, as is one fossil. Only one Recent species is found in

the eastern Atlantic (*H. doris* Röding = *H. rosea* Lamarck) and one in the eastern Pacific (*H. crenata* Swainson). Two fossil species come from the Miocene of Europe, and of course, the two Caribbean and eastern Pacific forms mentioned above as the New World fossil record.*

The only described species of *Harpa* in the Caribbean is that one originally referred by Gabb (1873, p. 214) to the West African "*H. rosea*" and subsequently renamed *H. americana* by Pilsbry (1922, p. 337). Known only to come from the Dominican Republic, with neither exact locality nor stratigraphic level being certain, and based upon a single incomplete shell, *H. americana* for some time remained the only name considered for any example of *Harpa* in the Neogene of the Caribbean. Thus, when Perrilliat Montoya (1960) monographed the "Middle Miocene" fauna of the Agueguexquite Formation of Mexico, the species of *Harpa*, which occurs in some numbers in the formation, was referred to *Harpa americana*. In 1979, Gibson-Smith and Gibson-Smith cited the *Harpa* they found in the Lower Miocene Cantaure Formation of Venezuela as "*Harpa* cf. *americana*." In 1981, Pitt attributed a specimen from the Pliocene beds at Esmeraldas, Ecuador, to *H. americana*,

*While this paper was in press the writer learned that David Dockery is in the process of describing a new species of *Harpa* from the Byram Marl (Vicksburgian - Lower Oligocene) of Mississippi (Miss. Dept. Nat. Res., Bur. Geol., Bull. 124, in press). Although there are a number of similarities to *Harpa* s.s. the resemblances to *Eocithara* are such that questions are raised as to whether the Mississippi form is truly to be referred to *Harpa* s.s. In particular, the inter-rib area is strongly cancellate and the protoconch seems to consist of only two rounded whorls. However, there is a thin callus that is not margined and that does overlay the ribs of the previous whorl in typical *Harpa* fashion. This Oligocene species seems to be in transition between *Eocithara* and *Harpa* but it does not appear to be closely related to any subsequent species of *Harpa*, either in the Old World or the New. It probably represents a parallel development in *Eocithara* that led to a dead-end.

thereby extending not only the geologic range but also the geographic range.

However, the Cantare specimens were soon removed from the synonymy of *H. americana* by Gibson-Smith and Gibson-Smith (1982) and referred instead to *H. myrmyia* Olsson, which had the effect of shortening the geologic range considerably, as the so-called "Middle Miocene" Agueguexquite Formation is now known to be Middle Pliocene (Akers, 1972, p. 30) and the Dominican beds from whence *H. americana* is assumed to have been collected are now known to be latest Miocene-basal Pliocene in age (Saunders et al., 1980, p. 157).

So long as the sole example of *H. americana* from the Dominican Republic was the incomplete type specimen we were not in a very good position to determine which, if either, of the remaining references should continue to be included with *H. americana*. But, after nine trips to the Dominican Republic, over a period of seven years, in which a total of over 150 localities were collected, at long last our perseverance was rewarded on the tenth trip with a second small example of *H. americana*.

This new specimen is not adult but that proved to be an advantage, for it does still have preserved the protoconch (see pl. 1, fig. 7b), which has four and one-half sharply conical whorls, and a noticeably cancellate shell surface (see pl. 1, figs. 7a and 8). This is in contrast to the Agueguexquite species, which has a protoconch of three and one-half rounded whorls and a nearly smooth adult shell. Therefore, the Mexican form is not to be referred to *H. americana* and it is described below as *H. isthmica*, n. sp.

Meanwhile, a second example of the Ecuadorian "*H. americana*" was recovered by Pitt (see pl. 1, fig. 5) and this shows the nature of the shoulder, missing in the first specimen. This new shell has a doubled row of shoulder spines, very like that in the living *H. crenata* and it is concluded that the Ecuadorian form is much nearer to that species than it is to the Dominican or Mexican one.

Thus, in the Caribbean we now have three species of *Harpa*: the youngest being *H. isthmica*, n. sp., most like the Recent West African *H. doris*; *H. americana*, from the Dominican Mio-Pliocene, probably ancestral to the Recent West Coast *H. cre-*

PLATE 1

Figures

- 1-3. *Harpa isthmica* Vokes, n. sp.
 1. ($\times 1\frac{1}{2}$) USNM 377402 (holotype); height 32.8 mm, diameter 22.0 mm.
Locality: TU 1046. Agueguexquite Fm., Veracruz, Mexico.
 2. (2a - $\times 3$; 2b - $\times 10$; 2c - $\times 2$) USNM 377403 (paratype A); height 21.3 mm, diameter 12.4 mm.
Locality: TU 638. Agueguexquite Fm., Veracruz, Mexico.
 3. ($\times 1\frac{1}{2}$) USNM 377404 (paratype B); height of fragment 36.5 mm, diameter of fragment 30.4 mm.
Locality: TU 1046. Agueguexquite Fm., Veracruz, Mexico.
4. *Harpa doris* Röding
($\times 1$) Tulane Collection; height 55.8 mm, diameter 33.2 mm.
Locality: Ivory Coast, West Africa.
- 5, 6. *Harpa crenata* Swainson
 5. ($\times 1\frac{1}{2}$) CAS 60735; height 39.0 mm, diameter (incomplete) 19.8 mm.
Locality: Quebrada Camerones (=TU 1397). Esmeraldas Formation, Prov. Esmeraldas, Ecuador.
 6. ($\times 1$) Tulane Collection; height 55.0 mm, diameter 35.5 mm.
Locality: Mazatlán, Sinaloa, Mexico (fishermen).
- 7, 8. *Harpa americana* Pilsbry
 7. (7a - $\times 2$; 7b - $\times 10$) USNM 377397; height 23.0 mm, diameter 14.3 mm.
Locality: TU 1444. Gurabo Formation, Dominican Republic.
 8. ($\times 1\frac{1}{2}$) ANSP 4061 (holotype); height 33.3 mm, diameter 19.4 mm.
Locality: Unknown, Dominican Republic.

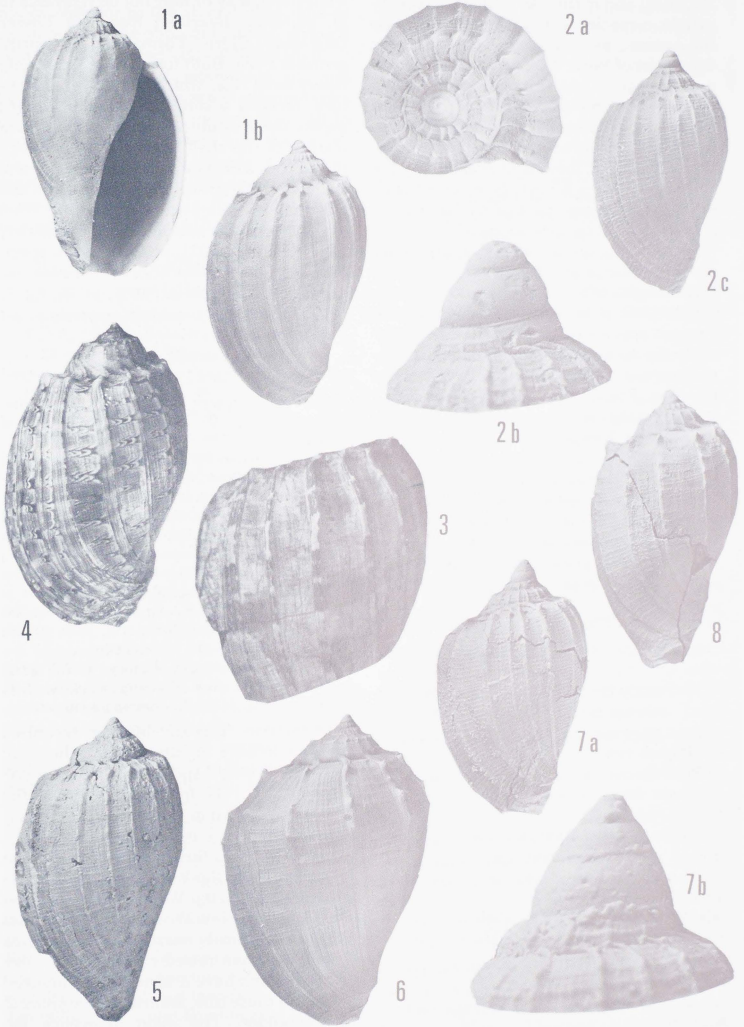


PLATE 1

nata and its mid-Pliocene relative in Ecuador; and in the early Miocene of Venezuela, a species which may or may not be the same as *H. myrmia*, from the Oligocene of Peru. The latter question cannot be resolved unless more material of the Oligocene form is recovered, for the unique type specimen is woefully incomplete. But, on the basis of the material presently available, there is no reason why the Venezuelan form is not to be referred to *H. myrmia*. Both are marked by having the suture crossed by extensions of the ribs, a feature that is not developed in any other species of *Harpa* now known.

Although Gibson-Smith and Gibson-Smith (1982, p. 59) suggested that the Venezuelan species might prove to be ancestral to the *H. crenata* line, the nature of the varices would seem to indicate this is not the case. For the present we will continue to assume that an as-yet unknown ancestor in the early Neogene gave rise to both *H. doris* and *H. americana*. In the New World, *H. americana* then gave rise to both the Mexican *H. isthmica* and the Ecuadorian *H. crenata*, the latter in turn persisting into the Recent fauna. The more southern lineage of *H. myrmia* is presumed to have left no descendants.

III. SYSTEMATIC DESCRIPTIONS

Superfamily VOLUTACEA Rafinesque, 1815

Family HARPIDAE Bronn, 1849

Genus HARPA Röding, 1798

Harpa RÖDING, 1798, Mus. Boltenianum, p. 179.

Type species (by tautonymy): *Harpa nobilis* Röding = *Buccinum harpa* Linnaeus.

HARPA MYRMIA Olsson

Harpa myrmia OLSSON, 1931, Bulls. Amer. Paleontology, v. 17, no. 63, p. 114(21), pl. 32(20), fig. 7.

[?] *Harpa* cf. *americana* Pilsbry. GIBSON-SMITH and GIBSON-SMITH, 1979, GEOS, no. 24, p. 22.

[?] *Harpa myrmia* Olsson. GIBSON-SMITH and GIBSON-SMITH, 1982, Tulane Stud. Geol. Paleont., v. 17, no. 2, p. 57, text figs. 1-3.

Discussion: As noted above, the specimens from the Lower Miocene Cantaure

Formation of the Paraguaná Peninsula, Venezuela, may or may not be referable to *H. myrmia*, described from the Lower Oligocene Chira Formation of northernmost Peru. Both forms have extremely heavy axial ribs, which cross over the suture, forming a series of lamellar flanges across the subsutural ramp. The surface texture of the shell is cancellate between the smooth axial ribs. The parietal callus is somewhat marginate and suggests that this line may be independently derived from the ancestral *Eocithara* line. In particular, Rehder (1973, p. 231, pl. 204) cites a specimen from the Middle Eocene of Texas (reproduced from Palmer, 1937, pl. 65, fig. 6) which seems very close to *H. myrmia*.

HARPA AMERICANA Pilsbry

Plate 1, figs. 7, 8

Harpa rosea Lamarck. GABB, 1873, Amer. Phil. Soc., Trans., (N. S.) v. 15, p. 214 (not of Lamarck).

Harpa americana PILSBRY, 1922, Acad. Nat. Sci. Phila., Proc., v. 73, p. 337, pl. 23, fig. 13.

NOT *Harpa americana* Pilsbry. PERRILLIAT MONTROYA, 1960, Paleontologia Mexicana, no. 8, p. 24, pl. 3, figs. 18, 19 (= *H. isthmica*, n. sp.).

Harpa americana Pilsbry. REHDER, 1973, Indo-Pacific Moll., v. 3, no. 16, p. 257, pl. 228.

NOT *Harpa* cf. *americana* Pilsbry. GIBSON-SMITH and GIBSON-SMITH, 1979, GEOS, no. 24, p. 22 (? = *H. myrmia* Olsson).

NOT *Harpa americana* Pilsbry. PITT, 1981, Tulane Stud. Geol. Paleont., v. 16, no. 4, p. 155, text fig. 1 (? = *H. crenata* Swainson).

Discussion: This species was described without locality or stratigraphic horizon, but now a single specimen has been collected at TU 1444, in the basal beds of the Gurabo Formation, regarded as uppermost Miocene or basal Pliocene in age.

In many ways the Dominican species is more similar to the West American *H. crenata* than it is to the West African *H. doris*. In both of the New World species the axial ribs are extremely narrow and low, being little more than raised ridges on the shell surface. Both have a series of pronounced nodes on these ribs, anterior to the spine at the shoulder. The main difference between the two forms, in addition to the protoconchs, is the more inflated whorl outline

in *H. crenata*, in which the secondary nodes anterior to the shoulder become as prominent as the shoulder spines, giving a "double-shouldered" aspect to the shell.

As the Mexican *H. isthmica* n. sp., and the Pacific *H. crenata* are contemporaries (both mid-Pliocene) they are assumed to represent parallel descent from the earlier *H. americana*. The Mexican species moved in the direction of heavier ribs and a smoother shell while the Pacific form moved toward a more inflated shape.

HARPA ISTHMICA E. H. Vokes, n. sp.

Plate 1, figs. 1-3

Harpa americana Pilsbry. PERRILLIAT MONTOYA, 1960, Paleontologia Mexicana, no. 8, p. 24, pl. 3, figs. 18, 19 (not of Pilsbry).

Harpa americana Pilsbry. REHDER, 1973, Indo-Pacific Moll., v. 3, no. 16, p. 258 (in part, reference to Veracruz specimens only).

Description: Shell of moderate size, with (?) five teleoconch whorls in adult (three or four in all specimens seen), rapidly increasing in size; protoconch of three and one-half smooth, inflated whorls, tilted slightly at an angle to main axis of shell, a small keel developed at periphery. Spiral ornamentation on early post-nuclear whorls of flat-topped bands, alternating in strength, about four pairs on first whorl, increasing in number but diminishing in strength with growth, body whorl covered with numerous (approximately five pairs in one mm) faint spiral bands, combining with even weaker axial growth lines to give a linen-like texture to shell surface, stronger in young specimens, evanescent to an almost smooth surface on larger specimens. Axial ornamentation beginning on first post-nuclear whorl with 14 to 19, but usually 16, narrow, straight riblets, on second whorl number increasing to between 17 and 20, but always more than on first whorl; third and successive whorls having either the same or slightly fewer ribs than the second, varying from 15 to 21 in number; initially no angulation at shoulder, beginning faintly on second and prominent by third whorl, with a small abaperturally directed spine at each rib; anteriorly a series of extremely weak nodes marking the crossing of other spiral bands. Aperture elongate, parietal wall, including siphonal fasciole, covered by a thin callus wash; outer lip somewhat flaring at posterior end; recurved anal notch at posterior end with a callus becoming more pronounced in each successive whorl, overlapping the suture

and previous whorl to an increasing degree, entire area anterior to shoulder spines covered by third teleoconch whorl. Color pattern similar to that of *Harpa doris*, with zigzag lines between ribs, overlain by irregular larger blotches over-riding the ribs.

Holotype: USNM 377402; height 32.8 mm, diameter 22.0 mm.

Type locality: TU 1046, Agueguexquite Formation, roadcuts on either side of Mexico Highway 180, 12 km (7.5 mi) east of junction with side road into Coatzacoalcos, Veracruz, Mexico (the same locality as Perrilliat Montoya's 180 m east of Km 11 on highway "Paralelo 18," which goes from Coatzacoalcos to Mascupana).

Paratypes: A) USNM 377403; height 21.3 mm, diameter 12.4 mm; locality TU 638; B) USNM 377404 (fragment); height 36.5, diameter 30.4 mm; locality TU 1046.

Discussion: As noted in the introduction, the form cited by Perrilliat Montoya (1960, p. 24) as "*Harpa americana*" is not that species. It differs from *H. americana* in having a more mammillate protoconch, with three and one-half whorls, in contrast to the conical, four and one-half whorl protoconch of *H. americana*. On the basis of the two specimens as yet known of *H. americana* the new species also has more numerous and heavier varices, and a smoother surface in the adult shell. The Mexican species is closer to the living West African *H. doris* Röding than is *H. americana* (which was originally identified as the African form), having a nearly identical protoconch and the smooth shell of the living form. The new species, however, differs in having more numerous ribs, which are much narrower than those in *H. doris*. In addition, some specimens, although not all (for example the one here figured, pl. 1, fig. 4), of *H. doris* have stronger secondary nodes on the ribs, anterior to the shoulder spine.

The number of lamellar axial ribs is extremely variable in this species, but the pattern of increase then decrease in successive whorls seems constant. Table 1 shows the number of ribs in a few paratype specimens. There are numerous examples of this species in the Tulane collections from the Middle Pliocene (Neogene zone N. 20) Agueguexquite Formation (TU 638-24 examples; TU 1046-14; TU 1347-2) but

TABLE 1
Number of axial ribs per whorl in *H. isthmica*

Whorl Number	TU 1046				TU 638		TU 1347
First	16	16	16	19	15	—	16
Second	19	18	18	20	19	19	19
Third	19	15	17	17	17	23	19
Fourth	—	—	—	—	17	21	—

most are somewhat broken and battered, suggesting that the species lived in a relatively shallow habitat. This is further corroborated by the fact that it has been taken nowhere else, even in localities that are geographically very close to these but slightly older (N. 19, "Concepción Inferior") and of a somewhat deeper facies.

Although a majority of the specimens are less than 40 mm in height, the fragmentary paratype illustrated to show the color pattern (pl. 1, fig. 3) indicates a maximum height of at least 50 mm, or approximately the same size as *H. doris*. The color pattern is also very close to that of *H. doris*, with the exception that the larger blotches override the ribs, rather than just being between the ribs, and there is no trace of the thin dark line that marks the ribs in *H. doris*. An attempt was made to bring out the color pattern in the fossils by means of ultra-violet light but it was not successful.

The color seen in the paratype is natural; the holotype also shows an original color pattern but has been whitened here to bring out details of ornamentation.

HARPA CRENATA Swainson
Plate 1, figs. 2, 5; text fig. 1

Harpa crenata SWAINSON, 1822, Catalogue Shell Coll. Bligh, Appendix, p. 5.

Harpa crenata Swainson. KEEN, 1958, Sea Shells Trop. West America, ed. 1, p. 431, fig. 663; 1971, Sea Shells Trop. West America, ed. 2, p. 620, fig. 1357.

[?] *Harpa americana* Pilsbry. PITT, 1981, Tulane Stud. Geol. Paleont., v. 16, no. 4, p. 155, text fig. 1 (not of Pilsbry).

Discussion: The specimen figured by Pitt (1981, text fig. 1) from the Pliocene Esmeraldas Formation of Ecuador is lacking the shoulder area and, thus, does not show the three-pointed angulation characteristic of the Recent *H. crenata*. However, a second example (pl. 1, fig. 5) taken later by

TABLE 2
Number of axial ribs per whorl in *H. americana*

Whorl Number	Holotype	TU 1444
First	13	15
Second	17	17
Third	?12	17

Mr. Pitt, and now in the collections of the California Academy of Sciences, does show a tendency toward this ornamentation, as well as the linen-like texture of the shell surface of this species. The Recent examples of *H. crenata* become very inflated in the adult stage (pl. 1, fig. 6) but juvenile shells have an outline virtually identical to that of the Esmeraldas example (compare text fig. 1A and 1B).

Neither of the Esmeraldas specimens has a perfect protoconch but the smaller example seems to show a mammillate protoconch of three and one-half whorls, which is identical to that of the Recent specimens of *H. crenata*. Therefore, on the basis of the two specimens currently available, there is no reason that the Esmeraldas form is not to be considered the same as the living form; it may be a stratigraphic subspecies, at best.

IV. ACKNOWLEDGMENTS

The writer is grateful to Mr. William Pitt, Research Associate of the California Academy of Sciences, and the Academy itself, for the loan of the two specimens from the Esmeraldas Formation utilized in this study. In addition, the Academy of Natural Sciences of Philadelphia kindly loaned the holotype of *H. americana*. Financing of the trip to the Dominican Republic, which finally produced a second example of *H. americana* was provided by the Mesoamerican Ecology Institute of Tulane University.

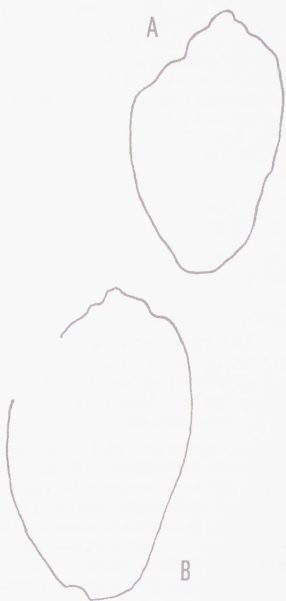
V. LOCALITY DATA

The following are Tulane University locality numbers:

638. Agueguexquite Fm., roadcut, pipeline cut, and quarry on Mexico Highway 180, 14 miles east of junction with side road into Coatzacoalcos, Veracruz, Mexico.
1046. Agueguexquite Fm., roadcuts on both sides of Mexico Highway 180, 7.5 miles east of junction with side road into Coatzacoalcos, Veracruz, Mexico. (This locality is that described in Perrilliat Montoya, 1960, *Paleontologia Mexicana*, No. 8, p. 5.)
1397. Esmeraldas Fm., Quebrada Camerones, cut bank on east side of canyon, which is at east edge of village of Camerones, 20 km (by road) east of highway bridge over Rio

Esmeraldas, at Esmeraldas, or approximately 5 km east of mouth of Rio Esmeraldas, Prov. of Esmeraldas, Ecuador (a shallow-water gravity flow into deep water Esmeraldas Fm.).

1444. Gurabo Fm., Rio Yaque del Norte, east bank, at Lopez, approximately 0.5 km upstream from mouth of Arroyo Lopez, between middle and lower hard limestone ledges.
1347. Agueguexquite Fm., pipeline cut, which parallels Mexico Highway 180, 7.5 miles east of junction with side road into Coatzacoalcos, Veracruz, Mexico (due north of TU 1046).
- R-492. Jaco Beach, Pacific coast, south of Puntarenas, Costa Rica.



Text figure 1. Outline of shell shape in: A) *Harpa crenata* Swainson, TU R-492; and B) *Harpa* cf. *crenata*, Esmeraldas Fm., Ecuador. Both $\times 1$.

VI. LITERATURE CITED

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REVIEW

THE UNITED STATES ENERGY ATLAS, by David J. Cuff and William J. Young. Published by Macmillan Publishing Co., Inc., New York, 1980, viii + 416 pp., illus., \$75.00

This volume locates and describes the amount and distribution of all energy sources, from non-renewable resources such as coal, petroleum, natural gas, and nuclear fuels, to renewable resources such as solar power, windpower, and biomass. Organized in eleven chapters and profusely illustrated, the book is primarily

concerned with illustrating the quantities and qualities of America's resources with comparative data analyses by state and region, consumption and transportation patterns, the position of the United States in world energy supplies, and practical evaluations of solar energy heating versus oil and gas heating, etc.

Over 200 maps, 150 graphs and figures, and dozens of diagrams and halftones are included along with a glossary and index. The nine by twelve inch format permits a pleasing appearance and useful scale for the illustrative maps and figures.

 —H.C.S.