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THE GENUS *TROPHON* MONFORT, 1810 (GASTROPODA: MURICIDAE) IN THE TERTIARY OF PATAGONIA

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ABSTRACT—Species of *Trophon* Montfort, 1810 are well known from Tertiary rocks exposed over a wide area of Patagonia. All nominal species referable to the genus were revised and, where necessary, synonymized. Valid species were redescribed and reillustrated, based on type material and additional material collected at other localities ranging from Península Valdés to south of the mouth of the Santa Cruz River (along the Atlantic coast of Patagonia) to Lake Pueyrredón (along the foothills of the Andes). Of the 17 nominal species, only six are considered valid, i.e., *Trophon sowerbyi* new name (replacement for *Fusus patagonicus* Sowerby, 1846 *in* Darwin non d'Orbigny), *Trophon santacruzensis* Ihering, 1897, *Trophon camachoi* new species, *Trophon leanzai* Brunet, 1997, *Trophon contortus* Brunet, 1997.

INTRODUCTION

THE GENUS Trophon Montfort, 1810 is an endemic genus reported living in waters along the coasts of southern South America and Antarctica. The type species, Trophon geversianus (Pallas, 1774), lives along the Atlantic coast between the provinces of Buenos Aires and Tierra del Fuego in continental Argentina and also around the Malvinas Islands and up the Pacific coast of Chile to at least Chonos Archipelago. This genus is widely mentioned in the literature (100 nominal species recorded from South America and Antarctica), as it is one of the most conspicuous elements of the extant molluscan fauna in this area. In addition to the recent taxa referred to *Trophon*, several fossil species also have been described, mainly from Tertiary rocks in Patagonia. As early as 1846, Sowerby described Fusus patagonicus (Sowerby in Darwin, 1846 = Trophon sowerbyi new name), from Tertiary rocks near San Julián in southern Patagonia. Ihering (1897, 1899, 1907), Pilsbry (1897), Ortmann (1899, 1902), Steinmann and Wilckens (1908), and Brunet (1997) also described fossil material referred to this genus. Because of poor preservation, in many cases it is very difficult or even impossible to be certain of generic identification for this material.

Having a thick, amorphous, calcitic layer of shell material (Petitjean, 1979; Do Campo, 1991; Kool, 1993), these gastropods stood a better chance of preservation than other groups of mollusks that obviously must have shared their geographic distribution throughout the Tertiary. Material assigned to *Trophon* has been sporadically mentioned in the geological literature throughout the twentieth century, but generally they lack descriptions or illustrations as well as precise stratigraphic information. This has only increased the confusion surrounding the proper taxonomic placement and geographical distribution of the material, thus hindering its biostratigraphical or paleobiogeographic potential.

Carcelles (1943, 1946) attempted to bring some order to the disarray generated after many years of using names without a clear comprehension of the taxonomic scope and proper nomenclatural precision. Carcelles's aim was only partially attained, however, in part because he was unable to examine as many specimens (including types) as would have been desirable, and in part because of inadequate knowledge available then on the anatomy and biology of extant species in the genus. In addition, his comments on fossil species lacked adequate knowledge of stratigraphic and geographic data, which were too general and imprecise to establish affinities among fossil taxa and their relationship to living forms. A clear understanding of fossil taxa must precede any explanation of the origin and distribution patterns observed in the extant species of this genus. In this paper, we attempt to shed light on this situation, circumscribing as closely as possible the existing nominal taxa based on fossil material. We describe new fossil taxa and illustrate type material of all fossil nominal species of *Trophon* described from earlier literature. In many cases the correct characterization of fossil taxa is difficult as specimens are missing many important features that are necessary for an accurate identification, particularly protoconchs and radulae. Vokes (1992) commented on the radulae of the extant Patagonian species and concluded that they could be useful to distinguish species. As our material in no case includes radulae, we have adopted a somewhat conservative point of view, keeping the number of nominal species within reasonable limits and accounting for the wide range of variation within species, a fact that is acknowledged for the living members of this genus.

MATERIALS AND METHOD

For this study we have used material housed in museum collections as well as specimens collected by us over the years. Among the museum collections revised are: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, **MACN-Pi**), Museo de La Plata (La Plata, **MLP**), The Natural History Museum (London, **NHM**), Facultad de Ciencias Exactas, Físicas y Naturales, Universidad de Buenos Aires (Buenos Aires, **CPBA**), Purdue University (West Lafayette, Indiana, USA, **P**), Academy of Natural Sciences of Philadelphia, (Philadelphia, USA, **ANSP**), Centro de Investigaciones en Recursos Geológicos (Buenos Aires, **CIRGEO-PI**, now in the **MACN**), Naturhistoriska Riksmuset (Stockholm, **NHR**), Facultad de Humanidades y Ciencias, Departamento de Paleontología (Montevideo, Uruguay, **FHC-DP**), and Museo Paleontológico "Egidio Feruglio" (Trelew, Chubut, Argentina **MPEF-PI**).

GEOLOGY

All eight species described herein come from rocks that range in age from Late Oligocene to ?Pliocene (and possibly Pleistocene) and are exposed in diverse localities from central and southern Argentina (see Figs. 1–3). The lithostratigraphic units that yielded the material also contain other mollusks, mainly oysters, pectinids, and other muricid gastropods, all of which have calcitic shells. In some instances, aragonitic material is preserved, and in those cases the molluscan fauna is extremely rich.

The earliest members of this genus appear in the San Julián Formation, exposed along the coast between Playa La Mina and just south of San Julián, and inland along the cliffs surrounding the Gran Bajo de San Julián. This formation was formally described by Bertels (1970, 1977), although it has been known since



FIGURE 1-General map of localities mentioned in text.



FIGURE 2-Map of collecting localities in the Peninsula Valdés area.

the nineteenth century as a richly fossiliferous unit. Darwin (1846) collected part of his material from it and Ameghino (1898) based his "Juliense" on the molluscan fauna contained in it; Ortmann (1902) also described material from here. Other authors (Camacho, 1967, 1974; Di Paola and Marchese, 1973; Manassero et al., 1997, among others) discussed different aspects of its geology. The age of this unit is believed to be Eocene-Oligocene (Bertels, 1975), Oligocene (Náñez, 1988), or more precisely Late Oligocene (Barreda, 1997e). The Gran Bajo Member was proposed by Bertels (1977) for the lower part of the section, comprising 23 m of dark reddish fine sandstones and siltstones exposed at the type locality, i.e., Gran Bajo de San Julián. Overlying this unit are 45 m of yellowish and brown-greenish medium to coarse-grained sandstones and biogenic limestones very rich in calcitic skeletal remains of invertebrates that Bertels (1977) designated as the Meseta Chica Member.

The Monte León Formation is far more widespread than the San Julián Formation and was formally proposed by Bertels (1970) as well. Mainly consisting of yellowish to gray tuffaceous fine sandstone and siltstone with a variable content of pyroclastic material, it outcrops along the coast of Santa Cruz south of Deseado and its equivalents probably reach as far north as Trelew and inland up to the foothills of the Andes. This unit contains a very rich molluscan fauna, representing a large proportion of the named species from the Tertiary of Patagonia, especially in the area near the mouth of the Santa Cruz River. The age of the Monte León Formation is generally considered to be Late Oligocene to Early Miocene (Bertels, 1980; Náñez, 1988; Legarreta and Uliana, 1994; del Río and Camacho, 1998). Bertels (1980) divided this unit into two members: the Monte Entrada Member (lower) and the Monte Observación Member (upper).

The El Chacay Formation (Chiesa et al., 1995) is probably equivalent (at least in part) to the Monte León Formation and is exposed in northwestern Santa Cruz in the vicinity of Lakes Posadas and Belgrano. This unit includes about 300 m of richly fossiliferous sandstone and tuffaceous sandstone, which were noted and collected by Hatcher (1897) with the marine invertebrates he collected described by Ortmann (1902). Riggi (1957) surveyed the area and Chiesa et al. (1995) proposed the formal name. Previously, the beds had been included in the Centinela Formation (Furque and Camacho, 1972), the type section of which is located south of Lake Argentino. The age of this formation ranges from Eocene to Miocene (Ortmann, 1902; Ihering, 1907; Feruglio,



FIGURE 3-Map of collecting localities in the San Julián region.

1949; Chiesa and Camacho, 1995; Casadío et al., 2000, 2001). Equivalent horizons exposed across the border in Chile (referred to the Guadal Formation) carry a similar fauna and are considered to be Late Oligocene–Early Miocene (Niemeyer et al., 1984; Frassinetti and Covacevich, 1999).

The Chenque Formation (Bellosi, 1990) is exposed in the area surrounding Comodoro Rivadavia and probably along the southern coast of the San Jorge Gulf. Based on palynomorphs and dinoflagellates, Barreda (1996, 1997a, 1997b, 1997c, 1997d) suggested a Late Oligocene–Early Miocene age for it. It is probably a northern equivalent of the Monte León Formation.

In the vicinity of Puerto Madryn, in the province of Chubut, the Puerto Madryn Formation (Haller, 1978) carries a rich fauna of mollusks that has been known since Darwin collected material there. This stratigraphic unit overlies the Lower Miocene marine Gaiman Formation and comprises about 100 m of interbedded yellowish sandstones, welded tuff, pebbly sandstones, richly fossiliferous shelly sandstones, and muddy or sandy shell beds (Haller, 1978; del Río, 1992). Fossils from this unit have been described by many different authors, most notably Ihering (1907), del Río (1992, 1994), and Brunet (1995, 1997). Del Río (1990, 1991) proposed a Middle Miocene age for the Puerto Madryn Formation based on the molluscan assemblages, whereas Scasso et al. (1999), using isotopic data, indicated an earliest Late Miocene (Middle Tortonian) age for the unit on Península Valdés.

At the southernmost end of the province of Santa Cruz, i.e., at the mouth of the Río Gallegos, a small outcrop of rocks overlying the continental Miocene Santa Cruz Formation was described by Hatcher (1897) as the Cape Fairweather Beds. Containing mainly pectinids and oysters, Hatcher collected a few specimens of a species of *Trophon*, which were described by Pilsbry (1897) and Ortmann (1902). These rocks are very restricted geographically and the age is still uncertain, although Hatcher and later authors (e.g., Feruglio, 1950) believed them to be Pliocene. No independent confirmation of such an age has been made and we consider the age assignment provisional. The relationship of this outcrop with others exposed along the coast further north, which also yielded specimens referable to *Trophon*, i.e., Monte Espejo and Sierra Laziar (or Laciar), is also obscure. The exposures at Sierra Laziar were considered equivalent to the Cape Fairweather sediments by Feruglio (1950); while he believed that the Monte Espejo terrace could be slightly younger, it is impossible to determine whether it is Pliocene or early Pleistocene.

In the delimitation of the fossil species within *Trophon* we have considered the fact that it usually becomes very difficult—because of the fragmentary nature of the fossil record and the high intraspecific variability inferred from that observed in the extant species—to distinguish lineages and identify properly the intervening taxa. Therefore, we have carefully considered the different variants of a continuous morphological spectrum appearing at the same locality and roughly the same stratigraphical unit before any decision on its taxonomic status was taken.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1797 Order NEOGASTROPODA Wenz, 1938 Family MURICIDAE Rafinesque, 1815 Subfamily TROPHONINAE Cossmann, 1903 Genus TROPHON Montfort, 1810

Polyplex PERRY, 1811 (type species Polyplex bulbosa PERRY, 1811 = Buccinum geversianum PALLAS, 1774).

Muricidea SWAINSON, 1840 (type species Murex magellanicus CHEM-NITZ, 1780 = Murex magellanicus GMELIN, 1791 = Buccinum geversianum PALLAS, 1774).

Type species.—Buccinum geversianum Pallas, 1774; by original designation.

Description.—Shells ranging from about 1 cm to more than 10 cm, fusiform, subquadrate to elongate. Protoconch with 2 to 2.5 slightly asymmetrical, smooth, and regularly convex globose whorls. Spire of four to six whorls, equal or slightly shorter than aperture height, never larger. Subsutural ramp generally present, slightly inclined posteriorly and defining conspicuous keel. Axial sculpture ranging from weak growth lines to strong lamellae, which in some instances might grow even over subsutural ramp. Lamellae along keel sometimes growing into strong open spines, which may curve backwards. Spiral ornamentation occasionally missing, but generally consisting of slightly rounded and equally developed cords, wider than interspaces and sometimes accompanied by weaker intercalated cords. Spiral ornamentation usually restricted to surface behind keel, while missing along subsutural ramp and in some cases only present in earliest whorls. Aperture subovoidal; outer lip sometimes slightly reflexed, but always smooth throughout. Siphonal canal always present and open. Pseudoumbilical chink generally present. Shell ultrastructure composed invariably of innermost layer of crossed lamellar aragonite, and outer layer of amorphous calcite. Relative thickness of both layers variable according to species.

Discussion.—The generic name Trophon has been widely used for nearly two centuries for a variety of species that, in many cases, has proved to belong in other genera. This situation exists because the original description and figures of the type species were very general, and the diagnostic characters used made it possible to include any number of forms that, under careful examination, could prove to belong in other groups. In addition, many of these characters refer to soft parts that are not preserved in the fossil material (Harasewych, 1984; Kool, 1993). We include here a redescription of shell characters for this genus and discuss differences in shell characters of other genera that include species mistakenly included in *Trophon*. The shell characters provided in our redescription are consistent with differences in soft parts that clearly distinguish the genus from other muricids.

The genus was introduced by Montfort (1810) for a species

living along the Atlantic coast of Patagonia (i.e., *Trophon geversianus*), the type species by original designation. Ever since, a large number of nominal species has been described, both fossil (17) and recent (104) from South America and Antarctica (Pastorino, 2002a). However, in most cases the high intraspecific variability went unnoticed and, in some cases, the poor preservation of the material casts doubt upon the names of many fossil species.

For example, a species such as *Trophon dubitans* Figueiras and Broggi, 1988 [1986] (p. 345–346, pl. 1, fig. 3; Fig. 4.3) was based upon a fragment of a poorly preserved external mold from the Camacho Formation (Goso and Bossi, 1966) along the Uruguayan coast of the Río de la Plata. The specimen only shows three whorls and a broken base, and the spire outline and ornamentation on the early whorl surface suggest that it might represent *Buccinanops* d'Orbigny, 1841. It cannot be included in *Trophon* as understood here.

Likewise, "*Trophon*" *broggii* Brunet, 1997 (p. 81–82, pl. 4, fig. 1) and "*Trophon*" *vokesae* Brunet, 1997 (p. 81, pl. 3, fig. 6), from the Puerto Madryn Formation in Valdés Peninsula, are probably a conspecific muricid belonging in an entirely different group. The types show short, strong shells with regularly spaced axial lamellae and strongly developed spiral ornamentation of primary and secondary cords. The spiral ornamentation lacks the "pitted" appearance present in those species of *Trophon* in which spirals are developed. Furthermore, some specimens develop a conspicuous labral spine, a feature that definitely removes them from the Trophoninae.

"Trophon"(?) *piramidensis* Brunet, 1997 (p. 82–84, pl. 4, fig. 2) is also a taxon that belongs in a group other than *Trophon*, as suggested by the weakly but distinctly lirate inner margin of its outer lip. The species probably belongs in the *Thais* clade sensu Vermeij (2001).

While not from Patagonia, *Trophon disparoides* Wilckens, 1911 (p. 29, pl. 1, fig. 33; Fig. 4.1, 4.2) is purportedly the earliest record for the genus. The only available specimen (i.e., the holotype) is a very worn and poorly preserved specimen from the Eocene La Meseta Formation in Seymour Island (Antarctica). The aperture is imbedded in rock and its systematic position must remain uncertain until better material becomes available.

Trophon paranensis Borchert, 1901 (p. 52, pl. 4, figs. 12, 13) is a species based on fragmentary material collected by Bravard (see Bravard, 1858) in Paraná (Province of Entre Ríos), from exposures of the Miocene Paraná Formation. Although Borchert illustrated a complete specimen, it was a reconstruction, as the original material was badly damaged. However, judging from his illustration and what little is left of the original, we can safely conclude that it belongs in another group of muricids, perhaps related to what Brunet (1997, p. 81–82, pl. 4, fig. 1) called "*Trophon*" *broggii* (="*Trophon*" *vokesae* Brunet, 1997, p. 81, pl. 3, fig. 6).

Trophon monoceros Ihering, 1907 (p. 183, pl. 14, fig. 92) is a species unrelated to *Trophon* and for which the subgeneric name *Entacanthus* Ihering, 1907 was proposed. It is probably close to *Ocenebra* Leach *in* Gray, 1847 sensu lato. Likewise, *Trophon pyriformis* Ihering, 1897 (p. 295, pl. 3, fig. 5) is a small, rather incomplete and strongly sculptured shell that probably is more correctly a member of the Ocenebriae as well.

The distinction between "primary" and "secondary" cords and denticles has been proposed by Merle (2001) and Merle et al. (2001) as a taxonomic character of the utmost importance within the Muricidae. While this appears to be a sound idea in the case of extant or very well-preserved fossil specimens—particularly within the Muricinae—it cannot be always applied to taxa represented by relatively poorly preserved material. This is the case of the Patagonian species, all of which include specimens that are either fragmentary or else missing the important early whorls,



FIGURE 4—1, 2, *Trophon disparoides* Wilckens, 1911, NHR1959, holotype, Graham Land, Seymour Island, Antarctica. 3, *Trophon dubitans* Figueiras and Broggi, 1988 [1986], FHC-DP2230 internal cast of the holotype, Barranca de San Pedro, Colonia, Camacho Formation, Uruguay. Scale bars = 1 cm.

crucial in the identification of primary and secondary cords. Therefore, the use of this character in this paper is severely limited. To avoid confusion, the terminology used for our material does not include the distinction between primary and secondary cords in the sense of Merle (2001). We only separate them in wide and narrow, two categories that imply a purely morphological distinction, regardless of the ontogenetic development of this feature. Perhaps further collections of specimens with early whorls and protoconchs preserved may in the future allow a detailed study in these lines.

It may be pointed out here that *Stramonitrophon* Powell, 1951 (type species *Trophon laciniatus* Martyn, 1784 = Murex plicatus Solander *in* Lightfoot, 1786)—originally proposed as a subgenus of *Trophon*—was based "solely on account of the dentition," which resembles that of *Stramonita* Schumacher, 1817 (type species *Buccinum haemastoma* Linnaeus, 1767). Identification of fossil material with Powell's subgenus is at present impossible, although the shells alone of *Stramonitrophon* and *Trophon* can hardly be distinguished from each other (Powell, 1951, p. 156).

TROPHON SOWERBYI new name Figure 5.1–5.15

Fusus patagonicus; G. B. SOWERBY, 1846, p. 259, pl. 4, fig. 60.
Trophon patagonicus SOW.; IHERING, 1897, p. 296 [non Murex patagonicus D'ORBIGNY, 1839 (=Trophon patagonicus), pl. 62, figs. 2, 3]; 1899, p. 31; ORTMANN, 1902, p. 215, pl. 34, fig. 7b-d, non figure a); CARCELLES, 1946, p. 77–79, fig. 10a-c; VOKES, 1991, fig. 17.

Description.—Shell fairly large, solid, rather thick-shelled; protoconch unknown; teleoconch of about six distinctly shouldered whorls; spire relatively high, approximately 50 percent of total shell height; aperture broadly oval; anterior siphonal canal very short, deep, and narrow, sharply inclined towards coiling axis; fasciole well developed; pseudoumbilical chink very deep and distinct; peristome evenly rounded, outer lip horizontal along sutural ramp, then widely rounded up to anterior siphonal canal; inner lip gently concave; outer lip slightly reflected; axial ornamentation of strong lamellae (about 10–13 on last whorl), sometimes formed by packing of weaker threads or lamellae; lamellae gives rise to flared backwards-pointing spine along peripheral keel; spiral ornamentation of very numerous and variably developed flat cords covering whorls below peripheral keel; cords sometimes very weak to almost obsolete, but always very closely packed, with a very narrow furrow between each other; intersection of spiral cords with weak axial threads rendering shell surface distinctly pitted.

Types.—Lectotype NHM G26415; paralectotypes NHM G26416 and NHM G26417. From Port San Julián (Patagonia).

Measurements.—Height of lectotype: 68.6 mm, width: 55.8 mm.

Other material examined.-MACN-Pi813, two specimens labeled Santa Cruz, Patagonia, "Lower Patagonian." MACN-Pi814, four specimens labeled Manantial Salado, "Lower Patagonian." MACN-Pi815bis, two specimens and a fragment from Fondo del Bajo "Lower Patagonian." MACN-Pi816, four specimens from Oven Point, "Patagonian." MACN-Pi826, four specimens from Cerro Pan de Azúcar, San Julián, "Lower Patagonian." MACN-Pi827, one specimen from Fondo del Bajo, San Julián, "Lower Patagonian." MACN-Pi4510, one specimen labeled Pan de Azúcar, "Lower Patagonian." MACN-Pi4511, two specimens labeled Manantial Salado, "Lower Patagonian." MACN-Pi4512, one specimen labeled Fondo del Bajo, "Lower Patagonian." MACN-Pi4520, two specimens from Manantial Salado "Lower Patagonian-Juliense." MLP4315, one specimen from San Julián, "Patagonian." MLP6804, six specimens labeled San Julián, "Juliense." MLP7362, five specimens labeled Grasería, San Julián, "Lower Patagonian." MLP7994, three specimens labeled San Julián, "Lower Patagonian." MLP9599, one specimen from Santa Cruz (?) "Patagonian." MLP9550, Cabo Curioso, Santa Cruz, "San Julián Formation." CPBA17321, one specimen from Playa de la Mina. CPBA17326, one specimen labeled Playa La Mina, Santa Cruz. CPBA17327, one specimen from Playa La Mina. CPBA17331, one specimen labeled Cabo Curioso, San Julián. CPBA6562, six specimens from Bajo de San Julián "Lower Patagonian." CPBA17335, 17336, 17337, 17325, one specimen each all from Playa La Mina. CPBA17342, 17343, one specimen each, both from Tumba Sholl "San Julián Formation." CPBA17333, one specimen, Cabo Curioso, Santa Cruz. CPBA17322, one specimen from Playa La Mina. CPBA17323, one specimen from Playa La Mina. CPBA17329, 17332, one specimen each, both from Cabo Curioso. CPBA17334, 17340, one specimen each, both from Cabo Curioso. MACN Pi4693, three specimens from Playa La Mina. MLP22508, four specimens from Gran Bajo de San Julián. MLP22621, three specimens from



FIGURE 5—Trophon sowerbyi new name. 1, 2, Fusus patagonicus G. B. Sowerby, 1846 in Darwin non d'Orbigny, lectotype NHM G26415; 3, MLP 7994, San Julián, "Lower Patagonian"; 4, 5, P 697, Oven Point, San Julián; 6, 7, P 697b; 8–10, P697a; 11, 12, MLP 23186, Playa de la Mina; 13–15, MLP 23180, Gran Bajo de San Julián.

Gran Bajo de San Julián. MLP22622, four specimens and fragments from Gran Bajo de San Julián. MLP23041, six specimens from Gran Bajo de San Julián. MLP23045, three specimens from Gran Bajo de San Julián. MLP23046, two specimens from Gran Bajo de San Julián. MLP23047, one specimen from Gran Bajo de San Julián. MLP23050, five specimens from Gran Bajo de San Julián. MLP23066, one specimen from Gran Bajo de San Julián. MLP23109, 11 specimens from Gran Bajo de San Julián. MLP23177, 11 specimens from Gran Bajo de San Julián. MLP23178, two specimens from Playa La Mina. MLP23179, one specimen from Gran Bajo de San Julián. MLP23180, one specimen from Gran Bajo de San Julián. MLP 23181, nine specimens from Gran Bajo de San Julián. MLP23182, 10 specimens from Gran Bajo de San Julián. MLP23183, 10 specimens from Gran Bajo de San Julián. MLP23184, nine specimens from Gran Bajo de San Julián. MLP23185, two specimens from Gran Bajo de San Julián. MLP23186, one specimen Playa La Mina. MLP23187, four specimens from Gran Bajo de San Julián. MLP23188, one specimen from Gran Bajo de San Julián. MLP23189, two specimens from Gran Bajo de San Julián. P697, three specimens from Oven Point, San Julián.

Occurrence.—Cabo Curioso, Playa La Mina, Gran Bajo de San Julián, Oven Point, Tumba Sholl, Manantial Salado; all localities in the vicinity of Puerto San Julián, Province of Santa Cruz, Argentina. All the material comes from the late Oligocene Meseta Chica Member of the San Julián Formation.

Discussion.—When first described, Sowerby (1846) did not designate a type and only illustrated one specimen. In order to fix the identity of this species, a new name is introduced here for this taxon and we designate specimen NHM G26415 as the lectotype. The other two specimens available to Sowerby (NHM G26416, NHM G26417) are designated paralectotypes. The type locality is, according to Darwin (1846), Port San Julián. He probably means the low cliffs along the coast just north of the town of San Julián (i.e., Oven Point or Tumba Sholl of later authors). Rocks exposed in this area are included in the Meseta Chica Member of the San Julián Formation. Most material in old collections is labeled "Lower Patagonian" or "Patagonian." Although the stratigraphic levels from which they were collected are somewhat uncertain, they also probably come from beds referable to the San Julián Formation.

Sowerby (1846, p. 259, pl. 4, fig. 60) believed *Trophon pata*gonicus was related to *Fusus lamellosus* [=*Murex lamellosus* Gmelin, 1791 = *Trophon plicatus* (Solander *in* Lightfoot, 1786)] and *Fusus magellanicus* [=*Murex magellanicus* Gmelin, 1791 = *Trophon geversianus* (Pallas, 1774)]. The specifc name, however, had been used by d'Orbigny (1839, pl. 62, figs. 2, 3) for a distinct species living presently off the coast of the province of Buenos Aires and northern Patagonia. Although d'Orbigny (1839, 1841) referred his species to *Murex* Linnaeus, 1758, close inspection of the type material reveals it belongs in *Trophon* (Pastorino, personal commun.). Hence, the requirement of a new name for Sowerby's species.

Trophon sowerbyi shares the strongly lamellose shell of *T. plicatus* but its lamellae are much lower and the shell has a distinctly subquadrate outline. Additionally, *T. plicatus* entirely lacks spiral ornamentation.

Trophon sowerbyi is generally provided with a fairly strong and peculiar spiral ornamentation, which at first glance appears similar to that of *T. geversianus*. However, the spiral cords in the type species are always very regularly spaced with wider furrows than in the Tertiary material. Furthermore, the shells of *T. geversianus* never show the "pitted" surface typical of *T. sowerbyi*. The sutural ramp is always present in *T. sowerbyi* and the shell outline is subquadrate, while in *T. geversianus* the shell is more distinctly biconical and the subsutural ramp is narrower and sometimes missing.

Although spiral ornamentation is a conspicuous shell character of *T. sowerbyi*, many specimens show extremely faint, or are missing, spirals. These two sculptural groups may represent two distinct species sharing the same habitat, as seen with the two extant species *T. geversianus* and *T. plicatus*. Sufficiently wellpreserved material is not available to assign the two morphologic groups to separate species with confidence.

Ihering (1897, p. 296) mentioned this species, stating that although he had not examined specimens, it was probably a variety of T. geversianus (Pallas). Ortmann (1902, p. 215, pl. 34, fig. 7ad), when discussing this species, included in it specimens that should be referred to other taxa. Three of his figured specimens resemble Sowerby's illustrated material (fig. 7b-d). We do not share Ortmann's opinion that his figure 7a corresponds closely to T. sowerbyi. Furthermore, this specimen probably does not belong in the Trophoninae at all. Ortmann (1902) also believed that Trophon laciniatus santacruzensis Ihering (1897, p. 294–295, pl. 3, fig. 4) was a synonym of T. sowerbyi (i.e., T. patagonicus Sowerby). Ihering (1907) refuted Ortmann, stating that he had mistaken T. patagonicus for T. laciniatus (=T. plicatus). At the same time he illustrated a specimen (Ihering, 1907, pl. 5, fig. 30) that can be undoubtedly referred to Sowerby's species. Although its resemblance to T. sowerbyi is not particularly close, it falls within the morphologic range of this very variable species.

Carcelles (1946) studied Ihering's collection and described and figured specimens that he correctly referred to *T. patagonicus*.

TROPHON SANTACRUZENSIS Ihering, 1897 Figure 6.1–6.8

Trophon laciniatus Mart. var. *santacruzensis* IHERING, 1897, p. 294, pl. 3, fig. 4.

Trophon laciniatus santacruzencis IHERING, 1914, p. 100.

Trophon (Austrotrophon) lamellosus (GMELIN, 1791); PARODIZ, 1996, p. 267.

Supplementary description.—Shell large (up to over 100 mm), biconic, very stout; protoconch unknown; teleoconch of five strongly shouldered whorls; spire about half of aperture height; all whorls except last one covering previous one almost up to keel in some specimens; suture abutting; aperture subovate; anterior siphonal canal rather long and deep; pseudoumbilicus deep and widely open; outer lip straight along shoulder, then becoming widely convex; inner lip gently concave towards aperture; axial ornamentation quite variable, some specimens almost smooth, others with more or less developed lamellae, others delicately but definitely lamellose; spiral ornamentation variably developed, always below keel and consisting of about 18 always very faint rounded cords separated by narrower grooves with barely visible additional narrower cords intercalated; entire shell surface generally covered by irregularly packed diffuse although conspicuous growth lines, which are more evident in interspaces, rendering these a somewhat "pitted" appearance; some worn specimens ornamented exclusively with lamellae and lacking entirely any trace of spiral ornamentation.

Types.—Ihering (1914) merely cited (and not expressly designated: ICZN Art. 74.5; Art. 74.6) MACN-Pi811 as "typus" and this does not constitute a lectotype designation (ICZN Art. 72.4.7). In order to fix the identity of *T. santacruzensis*, we designate specimen MACN-Pi811 as lectotype (ICZN, 1999 Art. 74.7); MACN-Pi812, three specimens designated here as paralectotypes—one of them lost presumably before 1914. From Yegua Quemada, on the Atlantic coast south of Monte León, province of Santa Cruz, Argentina.

Material examined .--- MLP1135, one specimen from Cañadón



FIGURE 6—1–8, Trophon santacruzensis Ihering, 1897. 1, 2, MLP 23194, Curva Makenke; 3, 4, MLP 23192, Curva Makenke; 5–7, MLP 23197, Curva Makenke; 8, Trophon laciniatus santacruzensis Ihering, 1897, lectotype MACN-Pi811. 9–13, Trophon camachoi n. sp. 9, 10, paratype CIRGEO-PI2188b; 11–13, holotype, CIRGEO-PI2182a.

Escobar, Bahía Solano, Chubut. MLP1145, one specimen from Bahía del Fondo, Santa Cruz. MLP1156, one specimen collected by J. Frenguelli in Punta Delgada. According to the label, which may be in error, the locality is in the province of Santa Cruz. The specimen comes from the "Leonense" which would be Miocene in age, but as there is no known locality called Punta Delgada in Santa Cruz, this reference must be considered at least doubtful. MLP2608, 2609, three specimens under each number from Cerro Chenque in Comodoro Rivadavia, province of Chubut, also from the "Leonense" (Chenque Formation of Bellosi, 1990). MLP4115, one specimen from Punta Borja, province of Chubut. MLP6973, one specimen from Rada Tilly, Chubut. MLP23190, one specimen from Monte León beach. MLP23191, three specimens, Curva Makenke, Santa Cruz. MLP23192 one specimen, Curva Makenke. MLP23193, two specimens from Mount Entrance, Santa Cruz. MLP23194, one specimen, Curva Makenke. MLP23195, 10 specimens from Curva Makenke. MLP23196, three specimens, Telégrafo Mazaredo, Santa Cruz. MLP23197, one specimen from Curva Makenke. MLP23198, two specimens, Bajo La Pava, Santa Cruz. CPBA8524, one specimen from Cerro Chenque in Comodoro Rivadavia. CPBA8525, one specimen from Punta Borja, Chubut. CPBA17363, one specimen, Bahía Mazaredo, Santa Cruz. CPBA17365, 17366, one specimen each, Cabo Tres Punta, Santa Cruz. CPBA14371, one specimen from Las Cuevas (on the border between the provinces of Chubut and Santa Cruz). MACN-Pi4517, one specimen, South East of Punta Nava, Golfo San Jorge.

Occurrence.—Specimens from Cerro Chenque, Punta Borja, Rada Tilly and Las Cuevas (all in the province of Chubut, Argentina); and Bahía Mazaredo, Punta Nava, Bajo La Pava and Telégrafo Mazaredo (all three in Santa Cruz), come from the Chenque Formation (Bellosi, 1990), which is considered to be Late Oligocene–Early Miocene based on palynological data (Barreda, 1996, 1997a–1997d). Other material, including the types, comes from exposures in the San Julián–Santa Cruz area, i.e., Estancia Makenke, Yegua Quemada, Mount Entrance, and Monte León, from the late Oligocene–early Miocene Monte León Formation.

Discussion.—This species was described by Ihering (1897, p. 294, pl. 3, fig. 4) from a broken specimen from Santa Cruz. Ihering had four specimens available, but the only specimen he illustrated is a fragment of the abapertural part of the last two whorls. Of the other three specimens, only two were catalogued by Ihering (1914), the third (also from Yegua Quemada, the type locality) may have been lost between 1897 and 1914. Although the material on which the species is based is very poor, additional material collected from nearby the type locality and in other areas in Patagonia allows positive identification of Ihering's taxa.

This variable species is morphologically very similar to the type species of the genus, i.e., *T. geversianus*. However, this species is generally larger, reaching up to over 100 mm, while specimens of *T. geversianus* rarely attain a size of 80 mm (except specimens collected in deep water). Another difference is the subsutural ramp, which is proportionally wider and smooth in *T. santacruzensis*. Spiral ornamentation, in the fossil species never attains the strength shows in *T. geversianus*. It seems also that the shoulder on the early teleoconch whorls is more clearly defined in the fossil species.

Trophon santacruzensis also resembles T. sowerbyi, but the spiral ornamentation is very faint in Ihering's species—even wanting on worn specimens. Furthermore, the characteristic fimbriate sculpture of most specimens of T. sowerbyi is never present in T. santacruzensis. This is noticeable even in poorly ornamented specimens of both taxa such as those depicted in Figure 6.5–6.7 (T. santacruzensis) and Figure 5.11, 5.12 (T. sowerbyi). Additionally, the subsutural ramp of T. santacruzensis is wider, smoother, and slightly convex, while in *T. sowerbyi* it is flat to slightly concave.

TROPHON CAMACHOI new species Figure 6.9–6.13

Trophon sp. CHIESA, PARMA, AND CAMACHO, 1995, p. 56, pl. 6, fig. 2.

Diagnosis.—Large, globose *Trophon* with strongly convex whorls; ornamentation of 9–12 strong flat spiral cords with fine growth lamellae closely packed and visible only within spiral interspaces; sutural ramp and shoulder missing.

Description.—Shell large, thick, globose, solid; protoconch unknown; teleoconch of at least five evenly convex whorls; spire moderately high for genus, about half of total height; aperture subovoid; anterior siphonal canal deep, short, and oblique; siphonal fasciole thick; umbilical chink shallow; outer lip evenly rounded; axial ornamentation poorly developed, sometimes low to almost obsolete irregular varices, even incipient variceal lamellae; very delicate growth lines; spiral ornamentation of strongly developed cords, about 9–12 on last whorl; cords of variable width and approximately equal in width to interspaces; intersection of spiral cords with growth lines and axial varices conveying a somewhat cancellate appearance to shell surface; growth lines becoming rather scaly within spiral interspaces.

Etymology.—This species is named after Horacio H. Camacho, who kindly loaned the studied material, for his contribution to study of Cenozoic mollusks from Argentina.

Types.—Holotype, CIRGEO-PI2182a; 17 paratypes CIRGEO-PI2182b-r. From Estancia El Unco, Lago Posadas, Santa Cruz.

Measurements.-Holotype: length: 80.6; width: 57.0.

Other material examined.—CIRGEO-PI2150 12 specimens, Rio Ceballos, northwestern Santa Cruz, El Chacay Formation; CIRGEO-PI1940a–b, two specimens, Estancia El Unco, northwestern Santa Cruz, El Chacay Formation. Camacho et al. (2000, p. 199, pl. 1, figs. 9, 10) also illustrated material they referred to *Trophon* sp., but this material belongs in a different group.

Occurrence.—All the material available was collected in beds referred by Chiesa and Camacho (1995) to the El Chacay Formation (previously included in the Centinela Formation of Furque and Camacho, 1972). According to Chiesa and Camacho (1995), this unit is Middle to Late Eocene. However, a more likely age is late Oligocene–early Miocene (Bellosi, 1995; Casadío et al., 2001).

Discussion.—The only species that shows any close resemblance to *T. camachoi* is *T. geversianus*. The extant *T. geversianus* is a variable species with some extreme forms provided with strong axial and spiral ornamentation and others almost smooth, with numerous intermediate forms. *Trophon camachoi* resembles specimens of *T. geversianus* with strong spiral cords and axial lamellae. However, these specimens of the extant species are lacking the closely packed fine growth lamellae in the interspaces observed in *T. camachoi*. The Tertiary species also has more strongly convex last whorls and is totally devoid of shoulders or subsutural ramps, while these are commonly present to some degree in *T. geversianus*.

Although further studies are necessary to confirm this, the absence of *T. camachoi* from rocks of similar age exposed along the coast of Patagonia may be explained by the particular environmental conditions and paleogeographic setting in which the El Chacay Formation was deposited (Bellosi, 1995).

TROPHON LEANZAI Brunet, 1997 Figure 7.1–7.18

Trophon leanzai BRUNET, 1997, p. 78, pl. 3, fig. 1. Trophon retrorsum BRUNET, 1997, p. 79-80, pl. 3, fig. 5.



FIGURE 7—1–18, Trophon leanzai Brunet, 1997. 1, 2, holotype, MPEF-PI116; 3, 4, MACN-Pi4686 Cerro Avanzado, Puerto Madryn, Chubut; 5, 6, MPEF-PI120 (holotype of *T. quenselli* Brunet, 1997); 7, 8, MACN-Pi4687, Cerro Avanzado; 9, MACN-Pi4688, Cerro Avanzado; 10, MACN-Pi4689, Cerro Avanzado; 11, 12, MPEF-PI121 (holotype of *T. flinti* Brunet, 1997); 13, 14, MACN-Pi4690, Cerro Avanzado; 15, MPEF-PI118 (holotype of *T. michellii* Brunet, 1997); 16, MACN-Pi4691, Puerto Pirámides, 17, MACNPi4692, Puerto Pirámides; 18, MPEF-PI180 (holotype of *T. retrorsum* Brunet, 1997).

Trophon plicatus var. santacruzensis IHERING, 1897; BRUNET, 1997, p. 79, pl. 3, fig. 3.

Fuegotrophon flinti BRUNET, 1997, p. 84, pl. 4, fig. 3.

Xymenopsis quenselli BRUNET, 1997, p. 86, pl. 5, fig. 3.

Xymenopsis michellii BRUNET, 1997, p. 85-86, pl. 5, fig. 2.

Description.-Shell biconic, up to about 60 mm high, thin; protoconch unknown; teleoconch of four or five strongly shouldered whorls; spire high; suture abutting; aperture broadly polygonal; anterior siphonal canal long, deep, and curved; siphonal fasciole narrow and scaly; pseudoumbilical chink almost closed or reduced to very narrow and shallow slit; outer lip slightly reflected, straight along shoulder, at keel descending abruptly at angle slightly larger than 90 degrees and then curving itself inward to form anterior siphonal canal; inner margin of outer lip smooth; inner lip very lightly callused; axial ornamentation variable, almost entirely missing in some shells to fairly regular, stout, lamellose varices in others, ranging in number from 9 to 12; varices, when developed, tending to fade on shoulder surface in last two whorls; spiral ornamentation of flat narrow ribs below keel, numbering about 15 relatively wider ones with much narrower and weaker ones intercalated; ribs narrower than interspaces; ribs sometimes almost obsolete; surface of last whorl covered by evanescent axial fimbriae.

Types.—Holotype MPEF-PI116. From Punta Pardelas, Valdés Peninsula, province of Chubut, Argentina. From the Puerto Madryn Formation.

Other material examined.—MLP1155, two specimens, Puerto Pirámides, Chubut. MLP3080, one specimen, Punta Norte, Valdes Peninsula, Chubut. MLP3953, one specimen, Puerto Pirámides, Chubut. MACN-Pi4686, one specimen; MACN-Pi4687, one specimen; MACN-Pi4688, one specimen; MACN-Pi4689, one specimen; MACN-Pi4690, one specimen; MACN-Pi4694, 14 specimens; all from Cerro Avanzado, Puerto Madryn Chubut. MACN-Pi4691, one specimen; MACN-Pi4692, one specimen; MACN-Pi4695, 28 specimens, MACN-Pi4697, 14 specimens; all from Puerto Pirámides, Chubut. All material from the Puerto Madryn Formation.

Occurrence.—Cerro Avanzado, Province of Chubut, Argentina. From the Puerto Madryn Formation (beds A9-A12 of del Río, 1992).

Discussion.—Of the four new species referred by Brunet (1997) to Trophon s.s., only two can be considered valid. Trophon leanzai appears to be similar to earlier species of the genus, particularly Trophon sowerbyi, from which it differs by its taller spire in addition to having fewer and weaker lamellae as well as by lacking the pitted appearance of the shell surface produced by the spiral fimbriae on T. sowerbyi. Brunet (1997) mentions the presence of crenulations on the outer lip. However, these seem to be the expression of the outer spiral cords on the reflected portion of the outer lip. Fuegotrophon flinti, Xymenopsis quenselli, and Xymenopsis michellii are only variations of T. leanzai, a fact that becomes evident when an appropriate number of specimens are considered (see Fig. 7).

TROPHON CONTORTUS Brunet, 1997 Figure 8.1–8.10

Trophon contortus BRUNET, 1997, p. 80, pl. 3, fig. 4. *Trophon harringtoni* BRUNET, 1997, p. 78–79, pl. 3, fig. 2.

Description.—Shell of moderate size (up to 50 mm high), biconic; protoconch unknown; teleoconch of four or five strongly shouldered whorls; spire low, about one-third of aperture height; aperture broadly polygonal; anterior siphonal canal fairly long and narrow; siphonal fasciole narrow and scaly; pseudoumbilicus slitlike; outer lip straight along sutural ramp, then convex (at least in adult stages) down to base of anterior siphonal canal; inner lip not callused; axial ornamentation of about 9–14 lamellose varices, running along whorl surface from keel to base; varices very poorly developed on shoulders; lamellae projecting outwards and backwards along keel to form short broadly triangular open spines; spiral ornamentation variably developed, from very faint to strong, especially on larger specimens, consisting of fairly regular narrow flat cords, numbering over 10 on base of last whorl.

Types.—Holotype, MPEF-PI024 [*T. contortus*]; MPEF-PI124 [*T. harringtoni*]. From Punta Pardelas, Valdés Peninsula, Chubut, Argentina.

Other material examined.—MACN-Pi4696, two specimens; MACN-Pi4682, one specimen; MACN-Pi4683, one specimen; MACN-Pi4684, one specimen; MACN-Pi4685, one specimen; all from Cerro Avanzado, Puerto Madryn, province of Chubut, all from the Puerto Madryn Formation (beds A9-A12 of del Río, 1992).

Occurrence.—Cerro Avanzado, Province of Chubut, Argentina. From the Puerto Madryn Formation.

Discussion.—Trophon harringtoni Brunet, 1997 (p. 78–79, pl. 3, fig. 2) is only an extreme variation of *T. contortus* in which the shell has a similar—albeit subdued—ornamentation. This species resembles *Trophon santacruzensis* Ihering, 1897 (p. 294, pl. 3, fig. 4). However, the species from the Puerto Madryn Formation seems to have a shell with a more triangular profile and more conspicuous lamellae which are also slightly prosocline, as opposed to those of *T. santacruzensis*, which are slightly opisthocline. Furthermore, the spines along the keel of *T. contortus* are generally projected backwards. *Trophon contortus* can be distinguished from *T. leanzai* by its relatively shorter spire, subsutural shelf more nearly horizontal, and generally more triangular shell profile.

TROPHON INORNATUS Pilsbry, 1897 Figure 9.1–9.16

- *Trophon inornatus* PILSBRY, 1897, p. 330, text fig. unnumbered; IHERING, 1907, p. 402; 1914, p. 99.
- Trophon varians Orb. var gradata; IHERING, 1897, p. 297.
- Trophon laciniatus MARTYN; ORTMANN, 1902, p. 217, pl. 34, fig. 8a, b (non 8c).
- *Trophon laciniatus* var. *inoratus* (PILSBRY); ORTMANN, 1902, p. 218, pl. 34, fig. 8c. (not Ihering's 1897 material, which Ihering himself included in his synonymy and probably is *Trophon fairus* since it is "*transvesim costata*").
- Trophon inornatus fairus IHERING, 1907, p. 402; 1914, p. 100 (syntypes of Trophon inornatus fairus).
- Trophon inornatus gradata IHERING, 1907, p. 402.
- *Trophon varians* var. *gradata* IHERING, 1907, p. 403; 1914, p. 101; CAR-CELLES, 1943, pl. 3, fig. 11 (included in p. 434 as a synonym of *T. varians* d'Orbigny, 1841.).
- Trophon varians montenus IHERING, 1907, p. 404.
- *Trophon inornatus* IH.; CARCELLES, 1943, pl. 3, fig. 13 (included in p. 434 as a synonym of *T. varians* d'Orb.).
- *Trophon (Trophon) varians* (D'ORB.) 1841; CARCELLES, 1943, p. 431–437, pl. 3, figs. 8–10, 12 only.
- Trophon varians (D'ORBIGNY, 1841); PARODIZ, 1996, p. 240.
- Trophon (Austrotrophon) lamellosus (GMELIN, 1791); PARODIZ, 1996, p. 224.
- ?"Trophon" geversianus (PALLAS, 1774); MARTINEZ CHIAPPARA, DEL Río, AND REICHLER, 1998, p. 38, pl. 2, fig. 23.

Description.—Shell fairly globose, moderately to very thick and solid, up to 80 mm high; protoconch unknown, teleoconch of at least five strongly convex whorls; some specimens with somewhat shouldered whorls; shoulder placed at posterior third of whorl when present; spire height about half of aperture height; suture impressed; aperture subovoid; outer lip thickened in some specimens; anterior siphonal canal long and slightly to strongly sinuous; tip end of canal filled with layer of calcareous material;



FIGURE 8—1–10, Trophon contortus Brunet, 1997. 1–3, holotype, MPEF-PI024; 4, MACN-Pi4682 Cerro Avanzado, Puerto Madryn, Chubut; 5, 6, MACN-Pi4683, Cerro Avanzado; 7, 8, MPEF-PI124 (holotype of T. harringtoni Brunet, 1997); 9, MACN-Pi4684, Cerro Avanzado; 10, MACN-Pi4685, Cerro Avanzado.

siphonal fasciole enclosing fairly conspicuous pseudoumbilical slit; axial ornamentation variable, from totally smooth specimens to others with low irregular lamellose varices running along entire whorl surface and, when present, numbering 10; outer lip slightly reflected; spiral ornamentation missing.

Types.—Holotype ANSP948, from Cape Fairweather (Cabo Buen Tiempo), province of Santa Cruz, Argentina. Cape Fairweather Beds, Pliocene? to possibly Pleistocene.

Other material examined.—P704, Cape Fairweather, one specimen (Ortmann, 1902, pl. 34, fig. 8b). P704a, Cape Fairweather, one specimen (Ortmann, 1902, pl. 34, fig. 8a). P708, Cape Fairweather, three specimens, Tehuelche beds, Pliocene. P705, Cape Fairweather, four specimens. P706, Cape Fairweather, one specimen (Ortmann, 1902, pl. 34, fig. 8c). P707, Cape Fairweather, three specimens. MLP6123, Cape Fairweather, three specimens. MACN-Pi809, Araucano, Cabo Fairweather, Patagonia, Cotypus (Ortmann), one specimen. MLP23199 three specimens, Cabo Fairweather, Formación Cape Fairweather, Pliocene? MACN-Pi810, Cape Fairweather, Patagonia, two specimens (syntypes of *Trophon inornatus fairus* Ih.). MACN-Pi829, Araucano, San Julián, Patagonia (San Juan?) (the label says San Juan but it is probably San Julián), four specimens. MACN-Pi830, Araucano, Sierra Laziar between San Jorge and Deseado, 11 specimens. MACN-Pi831, Araucano, Monte Espejo, North of Río Seco, San Julián,



FIGURE 9—1–16, Trophon inornatus Pilsbry, 1897. 1–3, holotype ANSP948; 4–6, Trophon inornatus gradata Ihering, 1907, MACN-Pi810, syntype; 7, 8, P 704, Cape Fairweather (Ortmann, 1902, pl. 34, fig. 8); 9, 10, Trophon varians montenus Ihering, 1907, MACN-Pi834, syntype; 11, 12, P 706, Cape Fairweather (Ortmann, 1902, pl. 34, fig. 8c); 13, 14, P704a, Cape Fairweather (Ortmann, 1902, pl. 34, fig. 8a); 15, 16, Trophon varians montenus, MACN-Pi834, syntype.

three specimens. MACN-Pi833, Araucano, between San Jorge and Deseado, one specimen. MACN-Pi834, Monte Espejo, North of Río Seco, two specimens (syntypes of *T. varians montenus*).

Occurrence.—Monte Espejo, Cerro Laziar, Cape Fairweather. In all three localities it appears in rocks of approximately the same age, i.e., Pliocene? to possibly Pleistocene.

Discussion.--Several names have been used over the years for material belonging to this very variable species found in allegedly Pliocene sediments along the coast of Patagonia. The range of variation from strongly lamellose to completely smooth shells may lead to misconceptions when material is insufficient. Pilsbry (1897) introduced the name Trophon inornatus for two specimens collected by Hatcher at Cape Fairweather, in southern Patagonia. He also mentioned the presence of specimens he referred to Trophon laciniatus Martyn, which are probably only lamellose specimens of this taxon. At the same time, Ihering (1897) introduced the name gradata for a variety of Trophon varians from northern Santa Cruz. The exact provenance of this material is uncertain. The locality data furnished by Ihering (between San Jorge and Deseado) is too vague to attempt any identification of the type locality with confidence. Thus, we choose to use Pilsbry's name, even if the material is insufficient in both cases.

Ortmann (1902) considered that his material from Cape Fairweather could be placed in two different taxa, i.e., *Trophon laciniatus* Martyn and *Trophon laciniatus* var. *inornatus* (incorrectly spelled *inoratus* in the text). Both taxa, however, are representatives of the same species. Likewise, the subspecific epithets introduced by Ihering in 1907 (i.e., *Trophon inornatus fairus* and *Trophon varians montenus*) are intraspecific variations, evident when a suitable number of specimens is available.

Trophon varians d'Orbigny, 1839 (pl. 62, figs. 4–7; text in d'Orbigny, 1841, p. 452) was proposed for Recent specimens from Río Negro in northern Patagonia. D'Orbigny himself expressed some doubts as to whether it was or was not distinct from *T. geversianus*. In any event, d'Orbigny's species is quite similar but all specimens show at least traces of spiral ornamentation, a feature absent from *T. inornatus*.

The other extant species, *T. plicatus* (Solander *in* Lightfoot, 1786, p. 104) is completely different in outline and ornamentation. The shell and spire are proportionally taller and the lamellae, when present, are orthocline, while in *T. inornatus* they are prosocline. Shells of *T. inornatus* are lacking the spinose projections of the lamellae along the subsutural keel.

CONCLUDING REMARKS

The genus Trophon is perhaps the most conspicuous group of gastropods in the molluscan fauna of the Argentine shelf, along the coast of the southernmost tip of South America. The extant Trophon geversianus, type species of the genus, is very common from the province of Buenos Aires down to Tierra del Fuego and southern Chile. It lives in very shallow waters, even up to the intertidal zone. Most of the other species are also generally restricted to the shelf, although a few of them can reach greater depths. Being carnivorous, this species lives in connection with hard substrate byssate mytilids, generally in very shallow waters. Because of its feeding habits and the nature of its prey, populations of Trophon show little migratory movement. Trophon geversianus exhibits a large range of morphological variation, a fact also observed in other muricid species [e.g., "Thais" emarginata (Deshayes, 1839)] in which shell morphology is controlled genetically but in which the phenotypic expression can be modified by environmental conditions (see Palmer, 1982, 1985; McQuaid, 1996). All living species of the genus (in which larval biology is known) have lecithotrophic, nonplanktonic larvae, a fact that naturally restricts their dispersion. Presently there are no Patagonian species living in Antarctica nor Antarctic species living in Patagonia. Species referred to *Trophon* from Antarctica may conform to a different group, as they share unique characters that seem to point towards a possible generic differentiation (Pastorino, 2002a, 2002b). Occurrences of *Trophon* in areas other than Patagonia or Antarctica are doubtful.

A review of the fossil species referable to *Trophon* reveals that the earliest representatives that can be undoubtedly placed in this taxon come from rocks exposed along the Atlantic coast of Argentina, namely the Oligocene San Julián Formation in the province of Santa Cruz, southern Patagonia, Argentina. Reports of the genus from older rocks are doubtful. It is clear that the group originated in Patagonia and has been living uninterruptedly in the area ever since. Living species around Antarctica seem to be derived from the Patagonian stock. Although the Cenozoic fossil record in Antarctica is very incomplete, there has been no report of the genus from any of the marine units exposed there. Fossil species from elsewhere in the Southern Hemisphere referred to the genus, such as *Trophon(?) munitus* Marwick, 1934, from the Late Pliocene of New Zealand, seem to belong in other muricid genera not related to *Trophon*.

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