Journal of Paleontology, 93(5), 2019, p. 899–915
Copyright © 2019, The Paleontological Society
0022-3360/19/1937-2337
doi: 10.1017/jpa.2019.34

JOURNAL OF PALEONTOLOGY
A PUBLICATION OF THE Paleontological SOCIETY

New subfamily Indovolutinae and other volutids (Volutidae, Gastropoda) from the Eocene of Kutch, western India and their paleobiogeographic implications

Kalyan Halder and Shrestha Das

Department of Geology, Presidency University, 86/1 College Street, Kolkata 700073, West Bengal, India <kalyan.geol@presiuniv.ac.in> <shresthapresi@yahoo.in>

Abstract.—Seven species belonging to the gastropod family Volutidae are reported for the first time from Kutch, Gujarat, India. They are *Prestrombus* aff. *Prestrombus rockei* Cox, 1931, *Indovoluta humberti* (d'Archiac and Haime, 1854), *Indovoluta multidentata* (d'Archiac and Haime, 1854), *Involuta daviesi* Cox, 1931, *Involuta coxi* new species, *Athleta* (*Volutocorbis*) *harnaiensis* Cox, 1931, and *Lyria* cf. *Lyria punjabensis* Eames, 1952. Indovolutinae new subfamily, constituted of the Paleogene genera *Prestrombus* Douvillé, 1929, *Indovoluta* Eames, 1956, *Involuta* Cox, 1931, and *Lyrischapa* Aldrich, 1911, and the Cretaceous genus *Gosavia* Stoliczka, 1865, is proposed. These forms have elaborate development of columellar plaits. All of these genera evolved in the western part of the Indian subcontinent. They, except *Lyrischapa*, also largely remained restricted to this area. *Lyrischapa* flourished in the Americas after possibly migrating through the southern margin of the relict Tethys Ocean and crossing the Atlantic Ocean. It is argued that the geographic and temporal restriction of this new subfamily was due to lecithotrophic larval development.

UUID: http://zoobank.org/14bc056f-1d2e-4674-b624-9eb8e856a1f0

Introduction

The volutes (family Volutidae Rafinesque, 1815) are a very diverse group of gastropods. Their shell form and most other morphologies are strongly variable. In the definition of the family and in differentiating between members of it, however, columellar plaits have traditionally played an important role. This character is also quite variable in terms of number and strength (Pilsbry and Olsson, 1954). Columellar plaits are, however, not exclusive to this family. The feature is common in the superfamily Turbinelliodea Rafinesque, 1815 and the family Mitridae Swainson, 1831. It also independently evolved in the gastropod subclasses Opisthobranchia Milne Edwards, 1848 and Pulmonata Milne Edwards, 1848 (Price, 2001). Nevertheless, columellar plaits are most elaborately developed in some volutes including the type genus *Voluta* Linnaeus, 1758. Volutes are further distinguished from other prosobranch gastropods with columellar plaits in having stronger plaits toward the anterior part whereas in others they occur posteriorly.

Early researchers who pioneered the study of Cenozoic mollusks from the western part of the Indian subcontinent reported many typical volutids and some peculiar species that resemble members of different families except in having prominent columellar plaits (d'Archiac and Haime, 1854; Cossmann and Pissarro, 1909; Vredenburg, 1923, 1925; Douvillé, 1929; Cox, 1930, 1931; Eames, 1952). Most of these authors' monographs were based primarily on mollusks from Sindh and Balochistan of Pakistan with minor contributions from Kutch and Subathu in India (d'Archiac and Haime, 1854; Eames, 1952).

The Cenozoic marine sedimentary deposits of Kutch, Gujarat on the western coast of India include an almost continuous succession from the lower Eocene to the Holocene (Fig. 1). The first attempt to record mollusks from this succession was by Sowerby (1840), who briefly described and figured some species. Vredenburg (1925, 1928a) described the post-Eocene mollusks from western India, which at the time of publication included basins from Pakistan and western India. The majority of species that he described came from Pakistan. In recent times, the Oligocene and the Miocene gastropods from Kutch were reviewed by Harzhauser et al. (2009) and Kulkarni et al. (2010). The Eocene mollusks from Kutch, however, remained much less attended until recently except in some sporadic reports (Sastry and Mathur, 1968; Tandon, 1971; Tandon and Srivastava, 1980). More recently, they have started getting some attention from paleontologists (Kachhara et al., 2011a, b; Halder, 2012; Halder and Sinha, 2014; Halder and Bano, 2015).

The present authors intended to make a comprehensive systematic study of the gastropods from the Eocene of Kutch. Halder and Sinha (2014) recently reported the Eocene cerithioids (superfamily Cerithioidea Fleming, 1822) from Kutch. The present paper deals with volutids. Some species, which resemble members of other families in some diagnostic features but have elaborately developed volutid-like columellar plaits on their inner lips, are included. Paleobiogeographic implications of finding these animals in Kutch and other basins of the western part of the Indian subcontinent are also explored.

Geologic setting

The Kutch basin received a widespread, thick pile of sediments during much of the Mesozoic, followed by eruption of the Deccan Trap volcanics (Biswas, 1992). The resurgent sea started to

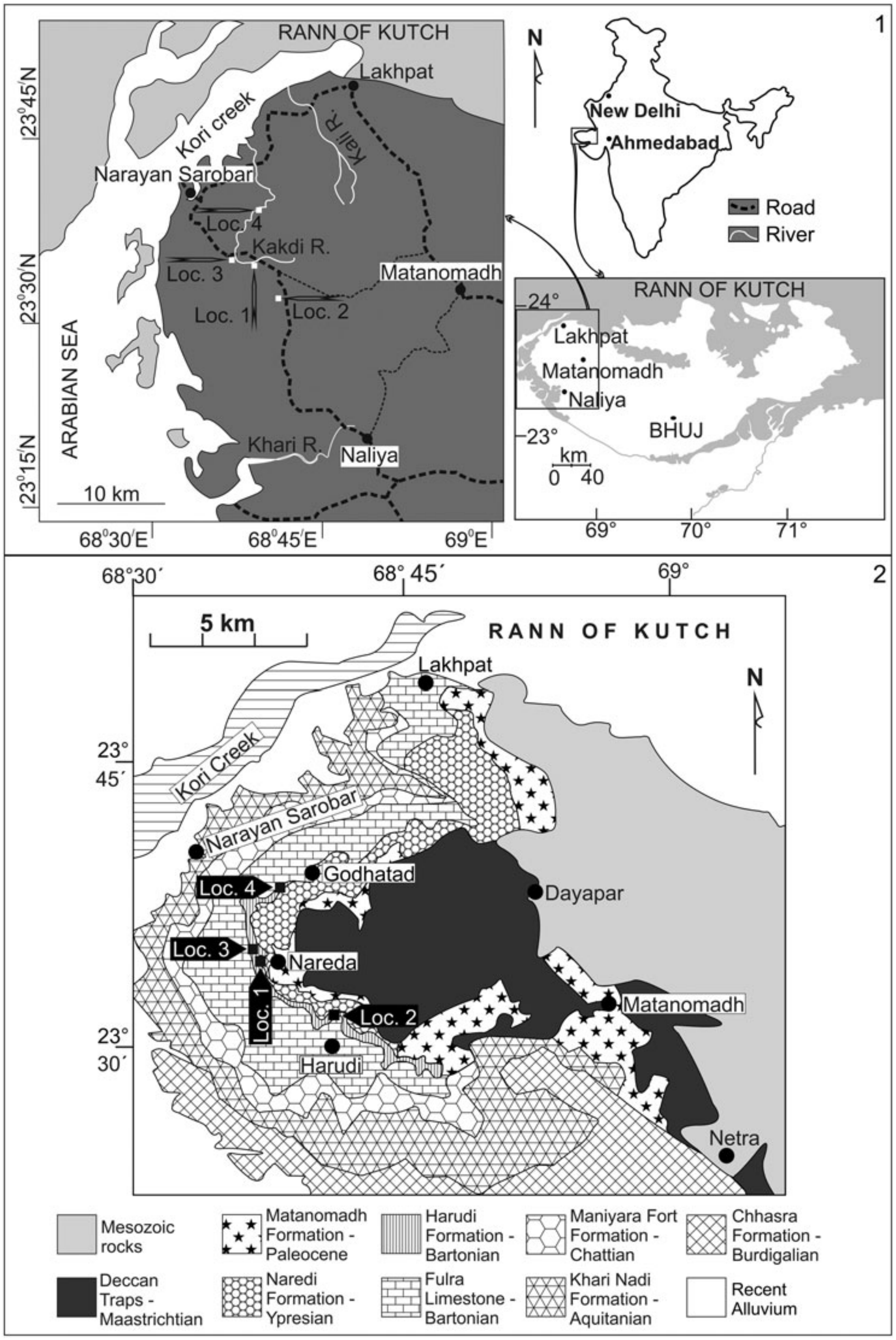


Figure 1. (**1**) Map of the area with collection localities demarcated. (**2**) Geological map showing fossil localities discussed in the text (modified after Biswas, 1992).

deposit fresh sediments during the lower Eocene (Ypresian) over the basement of the Deccan Trap or the Mesozoic sedimentary rocks (Biswas, 1992; Saraswati et al., 2016). There are, however, suggestions that Paleocene sediments are also present in Kutch (Tandon, 1971; Kachhara et al., 2011a).

Sedimentation initiated in the Kutch basin in a restricted environment under quiet conditions. Plane laminated shale is the motif of the basal unit, the Naredi Formation (Biswas, 1992), which was punctuated only once by a limestone bed studded with species of the larger benthic foraminifer *Assilina* d'Orbigny, 1839 (Fig. 2). Molluscan shells are found in the shales and the *Assilina* Limestone Member (Biswas, 1992). Because of poor induration of shales, the fossil shells are fragile and often difficult to retrieve. Fossils are preserved mostly as internal molds in the *Assilina* Limestone. They are also sometimes distorted.

The overlying Harudi Formation (Biswas, 1992) is also primarily argillaceous (Fig. 2). However, marine signatures are

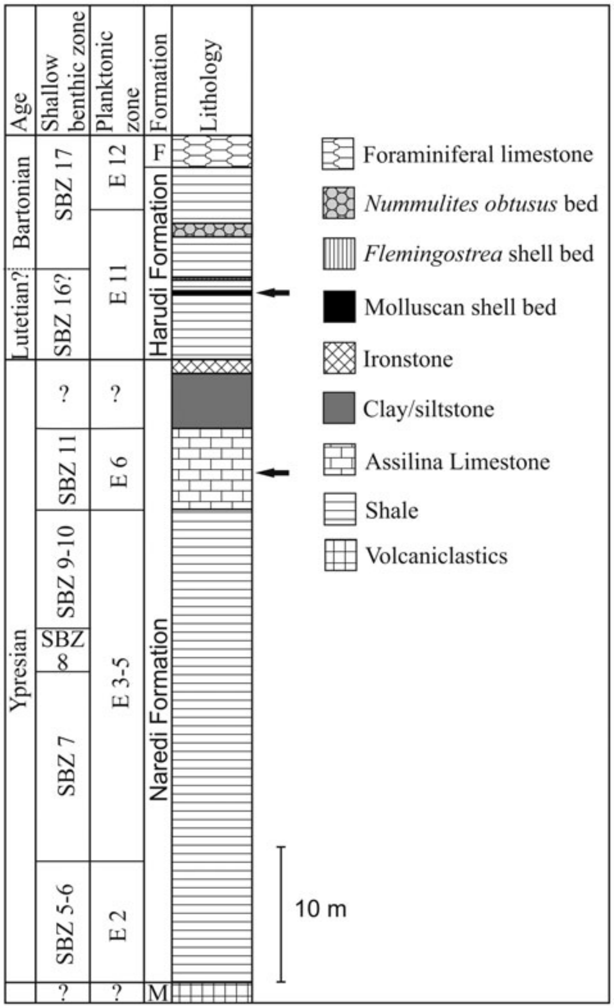


Figure 2. Composite lithostratigraphic section with collection levels marked by arrows. F = Fulra Limestone; M = Matanomadh Formation.

clearer here than in the Naredi Formation with several beds yielding abundant marine mollusks. A molluscan shell bed in the basal part of this formation is the most productive unit as far as well-preserved molluscan shells are concerned. The majority of species reported herein come from this bed. A persistent oyster bank occurs ~ 1 m above this shell bed. Near the top of this formation, another species of oyster is found in plenty. Megainvertebrate fossils are rare in the intervening portion of the formation. However, there is a thin, persistent foraminiferal limestone comprised of the larger benthic foram *Nummulites* spp. in this part. Oyster spats are found attached to them (Sengupta et al., 2011). Foraminiferal limestones, mainly characterized by the larger foram *Discocyclina* Gümbel, 1868, are also found below and above this bed. Deposition in this transgressive systems tract culminated in a thick foraminiferal limestone formation called the Fulra Limestone (Biswas, 1992; Catuneanu and Dave, 2017) (Fig. 2). The Harudi Formation and the Fulra Limestone are mainly deposits of the Bartonian age (Saraswati et al., 2016).

The Cenozoic formations outcrop in an arc surrounding the Deccan volcanics and the Mesozoic sedimentary rocks. They are roughly parallel to the present-day coastline (Fig. 1).

New subfamily Indovolutinae

Cox (1931) first noticed the uniqueness of a group of species with volute-like columellar plaits from the western part of the Indian subcontinent. These species resemble members of different families. He referred to their endemism but did not suggest an evolutionary relationship. Instead, Cox (1931) incorporated *Indovoluta* Eames, 1956 in the family Conidae Fleming, 1822 and *Involuta* Cox, 1931 in none, and retained *Prestrombus* Douvillé, 1929 in the family Strombidae Rafinesque, 1815. Douvillé's (1929) records of *Eovasum* Douvillé, 1920 and *Lyrischapa* Aldrich, 1911 (= *Diploconus* Douvillé, 1929; = *Diconomorpha* Wenz, 1943) were also included in the group by Cox (1931).

Givens (1991) suggested the necessity of a separate volutid subfamily to include the distinctive group of genera comprising *Indovoluta*, *Gosavia* Stoliczka, 1865, and *Lyrischapa*. The group flourished mainly in the western part of the Indian subcontinent during the Upper Cretaceous and the Paleogene. He re-assigned some volutid species from Pakistan to *Lyrischapa*. This genus is based on the type species *Lyrischapa harrisi* Aldrich, 1911 from the middle Eocene of America. Later, Merle et al. (2014) elaborated on *Lyrischapa* spp. from Pakistan. The genus *Eovasum* is regarded as belonging to the family Turbinellidae Swainson, 1835. However, *E. soudanense* Douvillé, 1920 was considered by Givens (1991) to belong to *Lyrischapa*.

Here we report volutid species from the Eocene of Kutch. None of these were previously known from Kutch. Many of these volutids resemble members of other families in some features. These unusual volutids belong to three genera—*Indovoluta*, *Involuta*, and *Prestrombus*. We have reviewed type specimens of many volutid species from Pakistan, e.g., the syntypes of *Prestrombus vredenburgi* Douvillé, 1929 (Fig. 3.1–3.4), the type species of the genus, the syntypes of *Lyrischapa elegans* (Douvillé, 1929), and the plesiotypes of *Lyrischapa haimei* (d'Archiac and Haime, 1854) (Fig. 3.5–3.9). Our observations and understanding of these genera and their allied forms, which led to the erection of Indovolutinae n. subfam., are discussed below.

Indovoluta *Eames, 1956*.—Eames (1956) erected the genus *Indovoluta* based on two Eocene species—*Indovoluta humberti* (d'Archiac and Haime, 1854) and *Indovoluta multidentata* (d'Archiac and Haime, 1854). These are reported here for the first time from Kutch and redescribed based on several specimens. The species were earlier placed in *Gosavia* (Cox, 1931; Eames, 1952), a distinct genus restricted to the Upper Cretaceous (Eames, 1956; Givens, 1991). *Gosavia* has a *Conus*-like low biconic shell. Its shell surface is characterized by reticulate ornamentation and its inner lip bears multiple columellar plaits in a volute-like arrangement. *Indovoluta*, resembling *Gosavia* in most respects except having a smooth shell and more numerous columellar plaits, appeared in the lower Eocene. Cox (1931) regarded *Gosavia* to belong to the family Conidae because of its extreme similarity in coiling pattern, shape, and subsutural anal sinus. These features commonly characterize the members of Conidae (Bouchet et al., 2011) but are not restricted to that family. Biconic to obconic shapes and subsutural sinuses are known from familiar volutid genera, e.g., *Athleta* Conrad, 1853 (Maxwell, 2003; Pilsbry and Olsson, 1954).

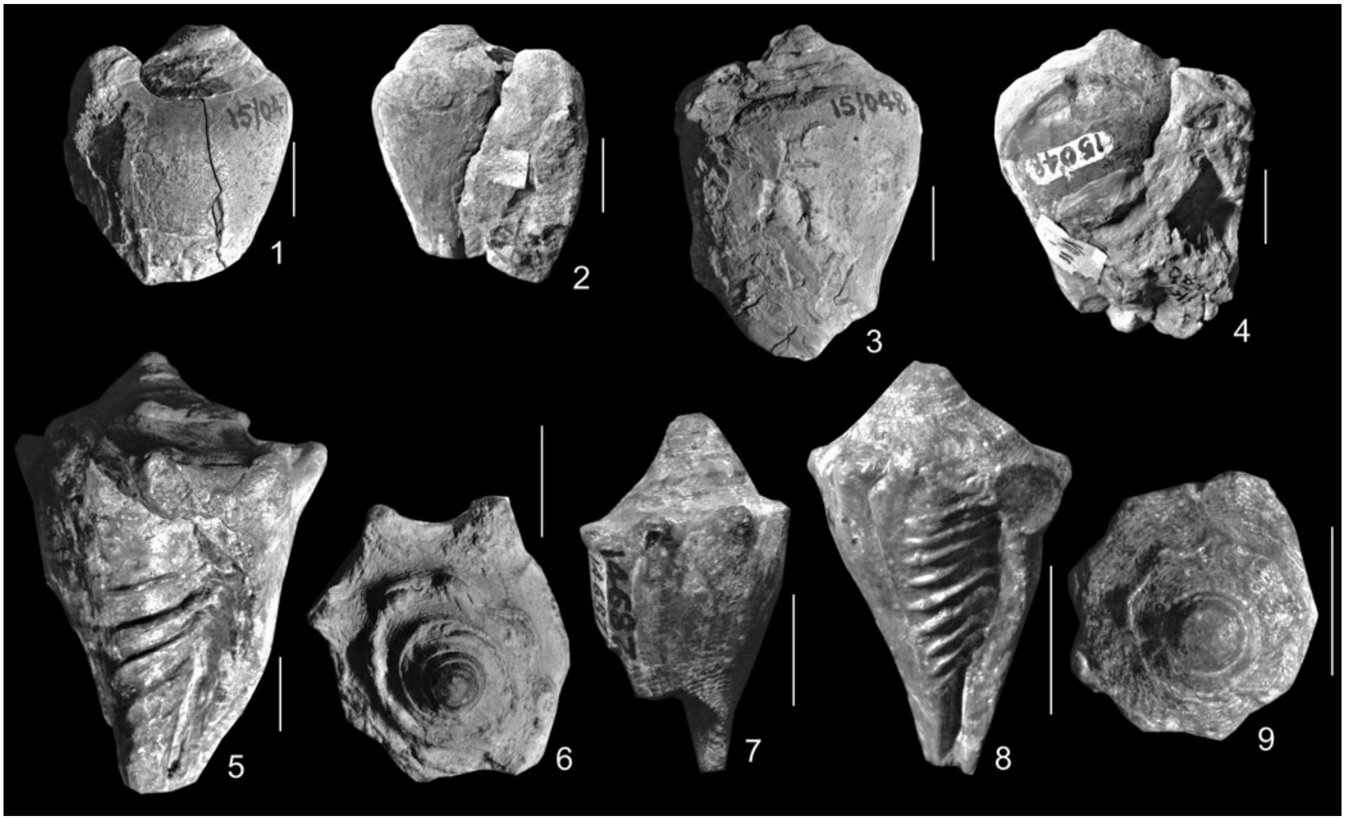


Figure 3. (**1–4**) *Prestrombus vredenburgi* Douvillé, 1929 from the lower Paleocene "*Cardita beaumonti*" beds of Sindh, Pakistan: (**1, 2**) syntype, GSI 15047, abapertural (**1**) and apertural (**2**) views; (**3, 4**) syntype, GSI 15048, abapertural (**3**) and apertural (**4**) views. (**5–9**) *Lyrischapa haimei* (d'Archiac and Haime, 1854) from the lower Eocene Hangu Shale of North West Frontier Province, Pakistan: (**5**) plesiotype, GSI 14685, apertural view; (**6**) plesiotype, GSI 14686, apical view; (**7**) plesiotype, GSI 14687, abapertural view; (**8, 9**) plesiotype, GSI 14688, apertural (**8**) and apical (**9**) views. Scale bars = 10 mm.

The contemporaneous genus closest in appearance to *Indovoluta* is *Lyrischapa*, which comes mainly from the Paleocene to the middle Eocene of America and Pakistan. *Indovoluta* lacks the shoulder tubercles and axial ornamentation of *Lyrischapa*. Spiral ornamentation on the shelf of *Lyrischapa* spp. also distinguishes them from *Indovoluta* spp. All other features of these two genera, including number and arrangement of columellar plaits, are similar. Some *Lyrischapa* spp. from Pakistan, however, differ from the middle Eocene type species from America in having distinct shell overlapping on the shelf. The posterior end of the whorl in some Pakistani species partially overrides the preceding shelf, thereby draping the shoulder and approximately half of the shelf of the previous whorl. Shoulder tubercles are commonly visible only on the last whorl (Givens, 1991, fig. 3.8, 3.10; Merle et al., 2014, figs. 5e, 6c, i). *Indovoluta humberti* from Kutch also clearly exhibits this overriding thick shell revealing only half of the shelf of the previous whorl and covering the trace of the anal sinus to a large extent (Fig. 4.7). *Lyrischapa* is known from 11 species that differ in ornamentation, degree of subsutural flexure, protoconch size, and coiling (Givens, 1979, 1991; Merle et al., 2014). Recently, Merle et al. (2014) reviewed *Lyrischapa* spp. from the lower Eocene of Pakistan. The genus *Lyrischapa* has been assigned to the family Volutidae although authors have been uncertain about its subfamilial affinities (Givens, 1991; Merle et al., 2014). *Indovoluta*, although close to *Conus* in shell shape, is closer to *Gosavia* and *Lyrischapa* in all features except ornamentation. Following Givens (1991), we assign this genus to Volutidae. The combination of low biconic shell shape, a distinct subsutural anal sinus on the shelf, and the elaborate arrangement of columellar plaits makes these genera unique among volutids (Table 1).

Involuta *Cox, 1931*.—It is difficult to assign the monospecific genus *Involuta* to any existing family because of its unusual characteristics, e.g., its long ovate shape, thin involute shell, parallel-sided crescentic aperture, and a series of sharp columellar plaits. Here we ascribe a new species to this genus, *Involuta coxi* new species, which has a convolute shell with no umbilicus on the apical side. Cox (1931) refrained from assigning the genus to any family pending discovery of specimens with preserved shells. We have several specimens of the type and only known species *Involuta daviesi* Cox, 1931. Most of the specimens are internal molds. However, the shell is visible in some places. On well-preserved internal molds, the thin shell left its impression, which we were able to reconstruct. Growth lines are essentially straight on the whorl side (Fig. 5.14). In early ontogeny, the shell bears reticulation (Fig. 5.21).

Cymbium Röding, 1798 (family Volutidae) superficially resembles *Involuta* in shape. It has wide ramp sloping toward the axis like that in *Involuta daviesi* (Smith, 1942; Landau and Marquet, 2000). However, its shell is not as involute as the latter, which has a deep apical umbilicus. *Cymbium* differs from *Involuta* mainly in the shape of the aperture and in having a strong siphonal

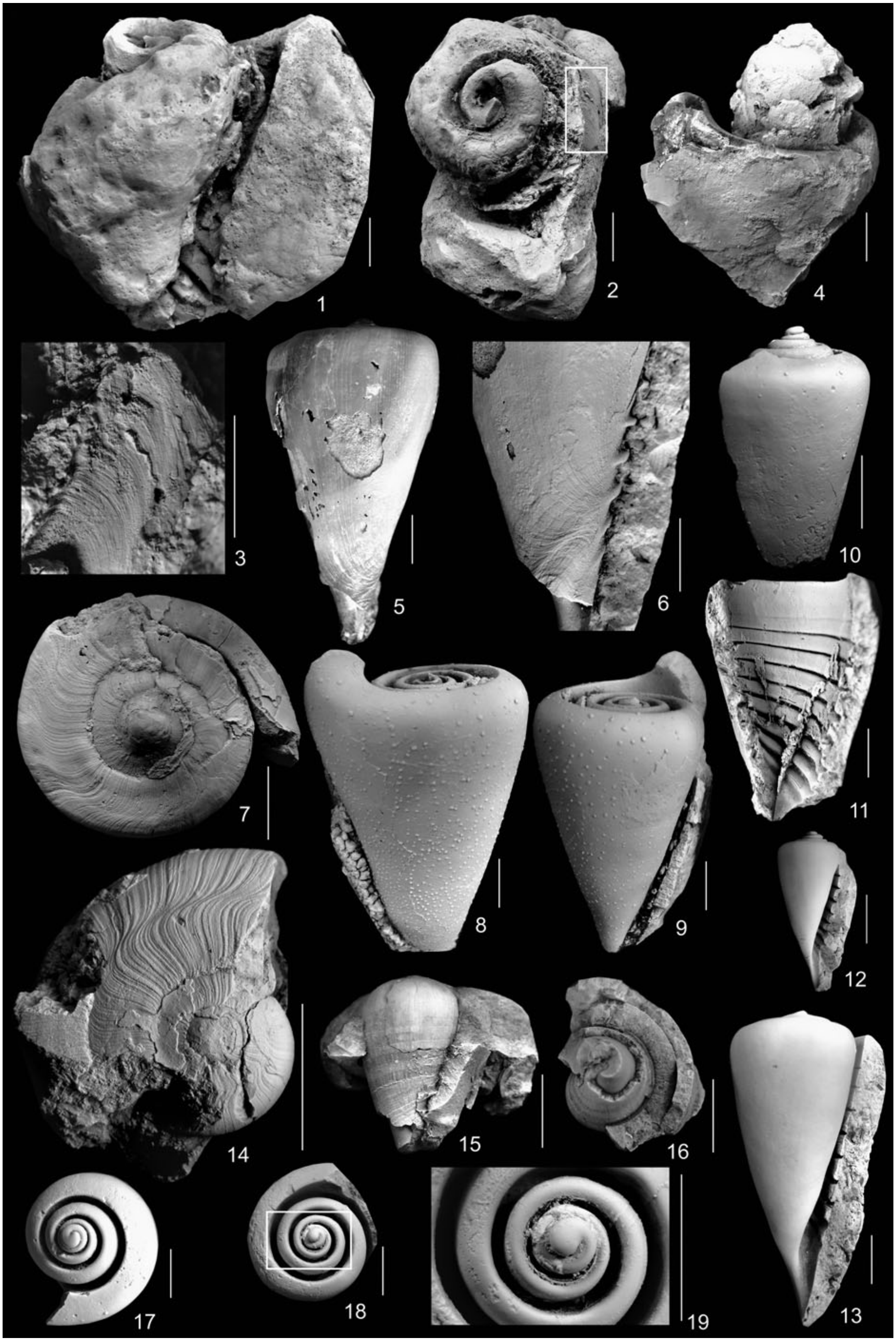

1
2
4
3
5
6
10
7
8
9
11
12
14
15
16
13
17
18
19

Table 1. Characters of the species belonging to the three genera of Indovolutinae n. subfam. discussed in the text.

Character	Species					
	Prestrombus vredenburgi	*Prestrombus* aff. *P. rockei*	*Indovoluta humberti*	*Indovoluta multidentata*	*Involuta daviesi*	*Involuta coxi* n. sp.
Maximum height (mm)	55.25	62	81	48.5	165	47.5
Shape	biconic	biconic	biconic	biconic	ovate	ovate
Diameter: height	0.57, narrow	0.95, wide	0.63, wide	0.37, very narrow	0.60, wide	0.55, narrow
Whorl overlap	>90%<100%	>90%<100%	>90%<100%	>90%<100%	>100%	100%
Position of suture	along shoulder	below shoulder	above shoulder	along shoulder	along shoulder	along shoulder
Anal sinus	unknown	middle of shelf	on shelf closer to shoulder	on shelf closer to shoulder	on shoulder	unknown
Shelf	inclined away from axis	inclined away from axis	inclined away from axis	inclined away from axis	inclined toward axis	narrow, horizontal
Shoulder	angular	angular	angular	angular, sharp	angular	weak
Width of aperture	relatively wide	relatively wide	narrow	narrow	narrow	narrow
Shape of aperture	rectangular	rectangular	rectangular	rectangular	crescentic	crescentic
Number of columellar plaits	< 6	< 6	8–10	8–10	~ 15	~ 15

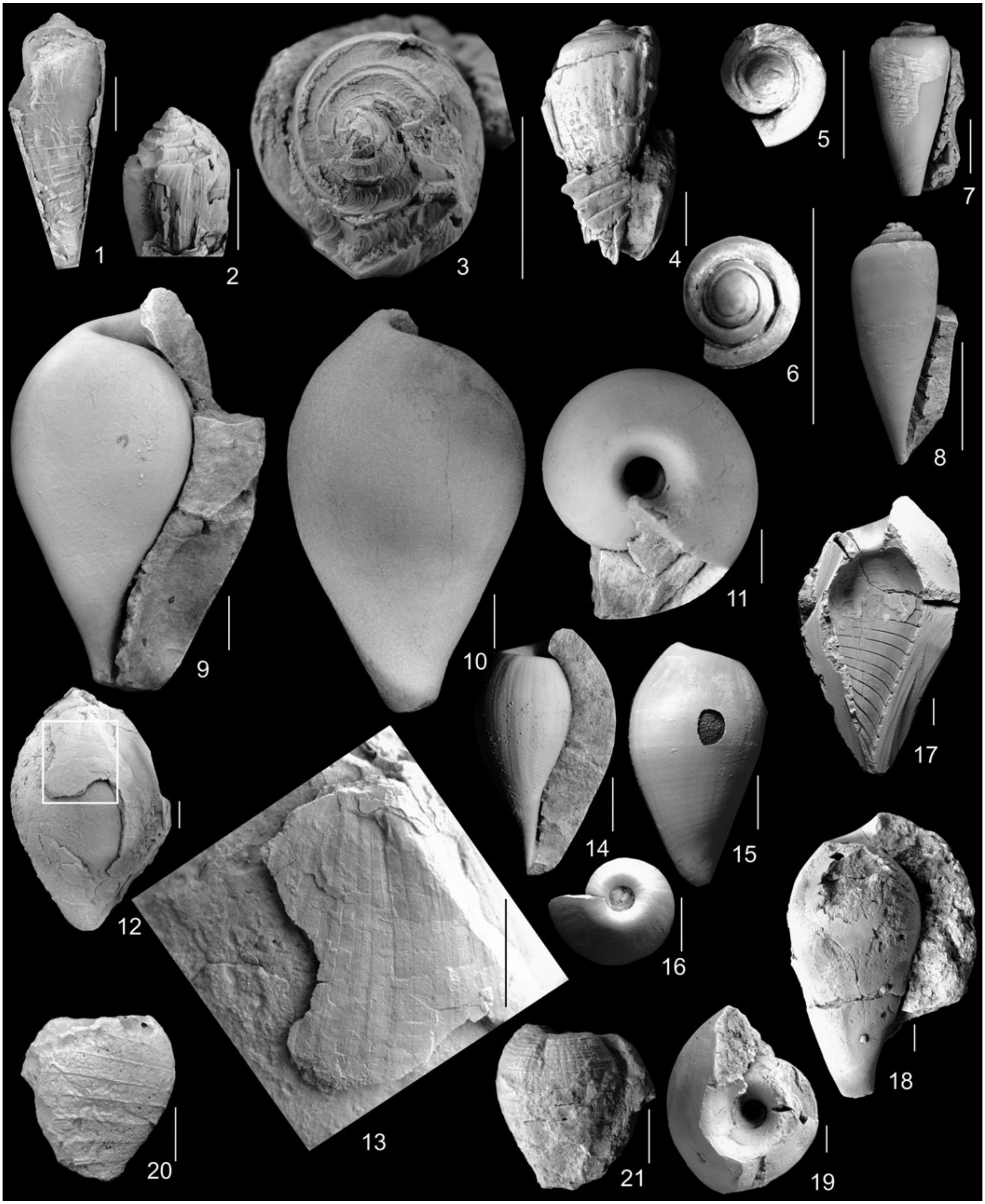
fasciole (Landau and Marquet, 2000). The aperture in the former is wide with the outer lip roughly parallel to the axis. The aperture of *Involuta* is crescentic with almost parallel-sided lips (Fig. 5.14). Columellar plaits are also much more numerous in *Involuta.*

In internal molds of *Involuta coxi* n. sp., the suture is slightly upturned along with a weakly constricted aperture and there is the suggestion of a faint plication on the interior of the outer lip. A slightly flared outer lip with a thickened interior produces an upturned suture in the internal mold. The flared, internally thickened, plicated outer lip is reminiscent of strombid gastropods (family Strombidae) (Savazzi, 1991). However, this similarity of apertural features appears to be superficial because *Involuta* does not resemble strombids in any other morphology, and such features are observed in other groups of gastropods including volutids (see e.g., Pilsbry and Olsson 1954; Maxwell, 2003). *Involuta* resembles unusual western Indian volutids much more closely in having a large, bulbous protoconch; a narrow, parallel-sided aperture; and an elaborate pattern of columellar plaits. Among these unusual gastropods from western India, development of columellar plaits is at its maximum in this genus. It has ~ 15 sharp plaits. Its ovate shape with a convolute to involute shell is also most distinctive among the members of this group (Table 1).

Prestrombus *Douvillé, 1929*.—The genus *Prestrombus* was erected based on *Prestrombus vredenburgi*, a lower Paleocene species from Sindh, Pakistan. The name suggests kinship with the family Strombidae. Douvillé (1929) considered this the oldest representative of the family Strombidae, but also noticed similarity with representatives of Muricoidea Rafinesque, 1815. The type species, represented by two internal molds (GSI 15047, 15048), shows a moderately upturned adult suture and strong columellar plaits (Fig. 3.1–3.4). The species is depressed having a wider aperture relative to those of *Indovoluta, Lyrischapa*, and *Involuta* (Table 1). However, its aperture resembles that of these genera in having nearly parallel-sided lips. It appears from the disposition of the suture and the preserved shell at places on the specimens that the shell was relatively thin. The only other species of the genus, *Prestrombus rockei* Cox, 1931, was also relatively poorly known and represented only by internal molds. Here we report the species from Kutch. Although the Kutch specimens are also poorly preserved, one of them exhibits a clearly defined shelf that is slightly inclined. Growth lines on the shelf flex back into the sinus (Fig. 4.3). The shell is very thick. The aperture of the species is wide but adapical extension of the suture is not prominent. Cox (1931) observed that its columellar plaits increase in strength from anterior to posterior, in contrast to the opposite trend found in volutes. In *Indovoluta*, *Involuta*, and *Lyrischapa*, we found that the most anterior plait is always quite weak followed by two relatively closely spaced strong plaits. Posterior to these, two or three plaits are more widely spaced and have almost equal strength. Strength decreases drastically thereafter. We observed, contrary to Cox (1931), that the pattern is similar in *Prestrombus*. Whereas several weaker plaits characterize the posterior part of the inner lip in the former genera, the total number of plaits in *Prestrombus* appears to be restricted to four to six (Douvillé, 1929; Cox, 1931).

Prestrombus, having similarity to other Paleogene Indian volutids in shape, patterns of growth lines, and columellar plaits, perhaps belongs to the same lineage. Adapical extension of the suture, which appears to be the primary reason for its inclusion in Strombidae, has also been observed in *Indovoluta* (Fig. 4.9), *Involuta* (Fig. 6.2), and other volutids (Pilsbry and Olsson, 1954; Maxwell, 2003, figs. 12, 28).

Figure 4. (**1–4**) *Prestrombus* aff. *Prestrombus rockei* Cox, 1931: (**1, 2**) PG/KG/Vl 64 from Loc. 1, Naredi Formation, apertural (**1**) and apical (**2**) views; (**3**) close-up of inset in Figure 4.2, preserved shell showing growth lines; (**4**) PG/KG/Vl 62 from Loc. 1, Naredi Formation abapertural view. (**5–19**) *Indovoluta humberti* (d'Archiac and Haime, 1854): (**5–7**) PG/KG/Vl 7 from Loc. 2, Harudi Formation, abapertural view (**5**), apertural view (in part) (**6**) showing columellar plaits, and apical view (**7**) showing shell overlapping on shelf; (**8, 9**) PG/KG/Vl 16 from Loc. 2, Harudi Formation, abapertural (**8**) and apertural (**9**) views; (**10**) PG/KG/Vl 6 from Loc. 4, Harudi Formation, abapertural view; (**11**) PG/KG/Vl 123 from Loc. 2, Harudi Formation, interior of the fragment of a whorl revealing columellar plaits; (**12**) PG/KG/Vl 23 from Loc. 2, Harudi Formation, apertural view; (**13**) PG/KG/Vl 17 from Loc. 2, Harudi Formation, apertural view; (**14–16**) PG/KG/Vl 3 from Loc. 4, Harudi Formation, apical view (**14**) showing trajectory of growth lines on shelf, apertural view (**15**), and basal view (**16**) revealing thick shell; (**17**) PG/KG/Vl 6 from Loc. 4, Harudi Formation, apical view showing large protoconch; (**18, 19**) PG/KG/Vl 19 from Loc. 2, Harudi Formation, apical view (**18**), and close-up (**19**) of inset in Figure 4.18 showing bulbous protoconch. Scale bars = 10 mm.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

Discussion.—It appears that *Prestrombus*, *Indovoluta*, *Lyrischapa*, and *Involuta* are unified by a prominent shelf and shoulder, an anal sinus on the shelf, a parallel-sided aperture, and several strong columellar plaits. They vary in degree of whorl overlapping, the position of the suture, depth and position of the deepest part of the subsutural sinus, width of the aperture, number of columellar plaits, and ornamentation. This Cenozoic group flourished mainly in the western part of the Indian subcontinent. The Cretaceous genus *Gosavia*, with similar characteristics, probably formed the rootstock. The purported descendants diverged in different directions. For instance in *Prestrombus*, the suture lies below the shoulder of previous whorl. The suture overrides the previous whorl in *Indovoluta* and *Lyrischapa*, and entirely drapes the previous whorl in *Involuta*. The anal sinus is at the shoulder in *Gosavia*. This state is retained in *Involuta*. In other Paleogene representatives, the sinus is on the shelf. Ornamentation varies from reticulate in *Gosavia* to almost smooth in *Prestrombus*, *Indovoluta*, and *Involuta*, and is characterized by shoulder tubercles and axial ribs in *Lyrischapa*. Reticulation in early ontogeny in the posterior part of *Involuta daviesi* demonstrates a possible evolutionary link (Fig. 5.21). Columellar plaits were seen to increase in number from four to six in early forms like *Gosavia* and *Prestrombus*, to 10–15 in later forms such as *Indovoluta*, *Lyrischapa*, and *Involuta*. We erect Indovolutinae n. subfam. for this unique and primarily Indian strain of volutid gastropods, with the genus *Indovoluta* as its type.

Key to the genera of Indovolutinae n. subfam.—

1. Biconic with rectangular aperture ———————— 2
1′. Ovate, involute to convolute, crescentic aperture with ~15 columellar plaits———————————*Involuta*
2. Columellar plaits < 6————————————————3
2′. Columellar plait > 6————————————————4
3. Ornamented (reticulate)—————————————— *Gosavia*
3′. Smooth——————————————*Prestrombus*
4. Ornamented (shoulder tubercles, axial ribs)——————— *Lyrischapa*
4′. Smooth——————————————————*Indovoluta*

Materials and methods

Specimens were collected from two stratigraphic levels and four localities. The *Assilina* Limestone Member of the Naredi Formation, exposed at the type section of this formation near the village of Nareda (Loc. 1, 23°34′32″N, 68°38′55″E) (Figs. 1, 2), yielded a few specimens. The shell bed in the basal part of the Harudi Formation (Fig. 2) yielded the rest of the specimens from three localities, one of which is the type section of the formation near the village of Harudi (Loc. 2, 23°32′N, 68°40′52″E) (Fig. 1). The other two localities of collection from this level are – Loc. 3, 3 km NW of Nareda, 23°35′03″N, 68°36′40″E and Loc. 4, 3 km WSW of the village of Godhatad, 23°38′37″N, 68° 38′21″E (Fig. 1). Specimens were coated with MgO before photography.

Repositories and institutional abbreviations.—All of the specimens from Kutch used here for systematic study are deposited in the Department of Geology, Presidency University (PG), Kolkata, India. Specimens are numbered with this institutional abbreviation, plus locality (K = Kutch) and taxonomic (G = Gastropoda, Vl = Volutidae) abbreviations. Other type specimens examined for this study are available in the Repository of Fossils of the Curatorial Division of Geological Survey of India (GSI), Kolkata. Type specimens of most of the existing species redescribed here are either in The Natural History Museum, London (NHM) or in the Geological Society of London (GSL).

Systematic paleontology

Class Gastropoda Cuvier, 1797
Subclass Caenogastropoda Cox, 1960
Cohort Sorbeoconcha Ponder and Lindberg, 1997
Subcohort Hypsogastropoda Ponder and Lindberg, 1997
Superorder Latrogastropoda Riedel, 2000
Order Neogastropoda Wenz, 1938
Superfamily Volutoidea Rafinesque, 1815
Family Volutidae Rafinesque, 1815
Subfamily Indovolutinae new subfamily

Type genus.—*Indovoluta* Eames, 1956

Diagnosis.—Large bulbous protoconch; teleoconch with 3–5 whorls; shape biconic to ovate, large whorl overlapping from > 90% to involute with development of apical umbilicus; generally with prominent shoulder; growth lines straight on whorl side, with sinus on shelf or shoulder; narrow parallel-sided aperture, rectangular to crescentic in shape; 4–15 elaborately developed columellar plaits; surface smooth to ornamented with spiral and axial ribs and shoulder tubercles.

Genus *Prestrombus* Douvillé, 1929

Type species.—*Prestrombus vredenburgi* Douvillé, 1929, lower Paleocene, Pakistan, by original designation.

Figure 5. (**1–8**) *Indovoluta multidentata* (d'Archiac and Haime, 1854): (**1–3**) PG/KG/Vl 89 from Loc. 3, Harudi Formation, abapertural view (**1**), close-up (**2**) showing elevated spire, angular shoulder, and straight growth lines on lateral side, and apical view (**3**) showing sinus on concave shelf; (**4, 5**) PG/KG/Vl 90 from Loc. 3, Harudi Formation, apertural view (**4**) exhibiting columellar plaits, and apical view (**5**); (**6**) PG/KG/Vl 97 from Loc. 3, Harudi Formation, apical view showing bulbous protoconch; (**7**) PG/KG/Vl 102 from Loc. 3, Harudi Formation, apertural view; (**8**) PG/KG/Vl 110 from Loc. 3, Harudi Formation, apertural view revealing columellar plaits. (**9–21**) *Involuta daviesi* Cox, 1931: (**9–11**) PG/KG/Vl 29 from Loc. 3, Harudi Formation, apertural (**9**), abapertural (**10**), and apical (**11**) views; (**12, 13**) PG/KG/Vl 30 from Loc. 3, Harudi Formation, abapertural view (**12**), and close-up (**13**) of inset in Figure 5.12 showing growth lines on whorl side; (**14–16**) PG/KG/Vl 121 from Loc. 2, Harudi Formation, apertural (**14**), abapertural (**15**), and apical (**16**) views; (**17–19**) PG/KG/Vl 26 from Loc. 2, Harudi Formation, interior of a separated part of the last whorl (**17**) revealing columellar plaits and straight growth lines, apertural view (**18**), and apical view (**19**); (**20, 21**) PG/KG/Vl 120 from Loc. 2, Harudi Formation, abapertural (**20**) and apertural (**21**) views showing details of ornamentation. Scale bars = 10 mm.

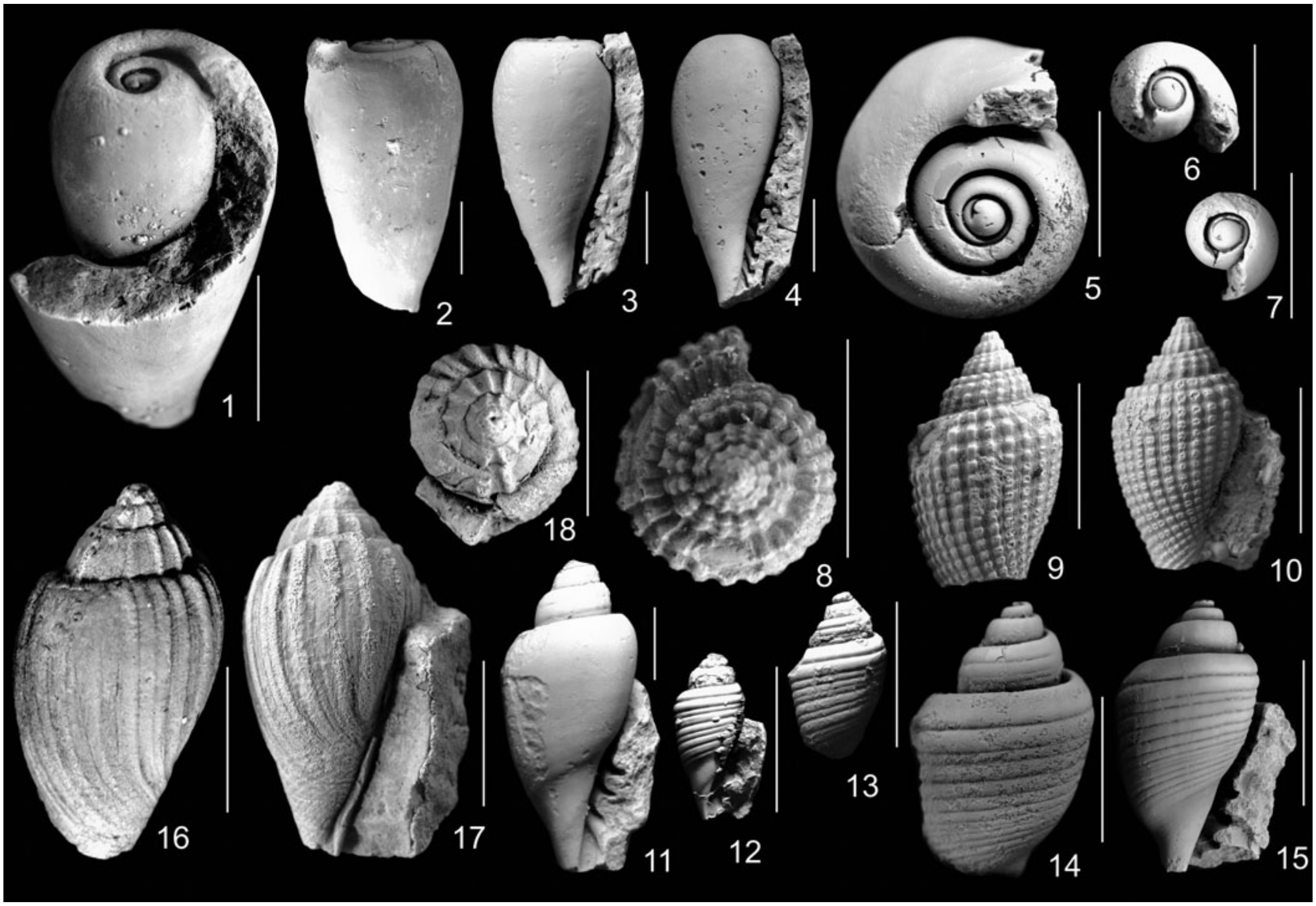


Figure 6. (**1–7**) *Involuta coxi* n. sp.: (**1**) paratype, PG/KG/Vl 117 from Loc. 3, Harudi Formation, lateral view; (**2–5**) holotype, PG/KG/Vl 42 from Loc. 3, Harudi Formation, abapertural view (**2**), apertural view (**3**), oblique apertural view (**4**) revealing columellar plaits, and apical view (**5**); (**6**) paratype, PG/KG/Vl 37 from Loc. 2, Harudi Formation, apical view; (**7**) paratype, PG/KG/Vl 119 from Loc. 3, Harudi Formation, apical view. (**8–15**) *Athleta* (*Volutocorbis*) *harnaiensis* Cox, 1931: (**8–10**) PG/KG/Vl 47 from Loc. 4, Harudi Formation, apical (**8**), abapertural (**9**), and apertural (**10**) views; (**11**) PG/KG/Vl 55 from Loc. 3, Harudi Formation, apertural view showing columellar plaits; (**12, 13**) PG/KG/Vl 59 from Loc. 3, Harudi Formation, internal mold showing prominent spiral ornamentation, apertural (**12**) and abapertural (**13**) views; (**14, 15**) PG/KG/Vl 122 from Loc. 2, Harudi Formation, abapertural (**14**) and apertural (**15**) views. (**16–18**) *Lyria*? cf. *Lyria punjabensis* Eames, 1952: abapertural (**16**), apertural (**17**), and apical (**18**) views. Scale bars = 10 mm.

Prestrombus aff. *Prestrombus rockei* Cox, 1931
Figure 4.1–4.4

1931 *Prestrombus rockei* Cox, p. 52, pl. 2, fig. 6.

Holotype.—NHM G.50252, lower Eocene, Sindh, Pakistan.

Occurrence.—Lower Eocene, Sindh and Punjab, Pakistan; lower Eocene, Khuiala Formation, Rajasthan; lower Eocene, Naredi Formation, Kutch, western India.

Description.—Large (largest specimen ~ 62 mm height, 59 mm diameter); wide, somewhat biconic with elevated step-like spire; protoconch unknown; teleoconch of ~ 4 whorls; last whorl large with convex side in posterior part and conical toward anterior; shell very thick; sutures prominently marked by wide gap in internal mold, running much below shoulder of previous whorl; shoulder angular; shelf wide, inclined, slightly concave in preserved shell; strong columellar plaits toward anterior part; posterior part of inner lip unknown; aperture wide, subelliptical, with nearly parallel-sided lips; growth lines with asymmetric subsutural flexure on shelf, unknown for remaining shell surface; suture showing vague tendency to rise posteriorly in latest part of whorl; basal constriction moderate.

Materials.—Three specimens (PG/KG/Vl 62–64) from the Naredi Formation exposed at Loc. 1; mostly internal molds with shell partially preserved.

Remarks.—The species is represented by a few ill-preserved specimens in our collection. It has its closest affinity to *Prestrombus rockei* from Sindh (Cox, 1931) in general shape and apertural features. However, the Sindh form is narrower than the Kutch form. Specimens of the latter are also much abraded. Hence, we place the Kutch form in open nomenclature. *Prestrombus* aff. *Prestrombus rockei* differs from *Prestrombus vredenburgi*, the type species from Pakistan, in having a thicker shell and less prominent posterior extension of the adult suture. The latter also comes from an older stratigraphic level of the lower Paleocene.

Genus *Indovoluta* Eames, 1956

Type species.—*Voluta humberti* d'Archiac and Haime, 1854, lower Eocene, Pakistan, by original designation.

Indovoluta humberti (d'Archiac and Haime, 1854)

Figure 4.5–4.19

1854 *Voluta humberti* d'Archiac and Haime, p. 327, pl. 34, fig. 9.
1854 *Voluta salsensis* d'Archiac and Haime, p. 328, pl. 34, figs. 10–11.
1908 *Voluta birmanica* Dalton, p. 632, pl. 57, fig. 10.
1931 *Gosavia humberti*; Cox, p. 57, pl. 1, fig. 18.
1937 *Gosavia humberti*; Vokes, p. 5, fig. 7.
1952 *Gosavia humberti*; Eames, p. 113.
1956 *Indovoluta humberti*; Eames, p. 109, pl. 22, figs. 1–3.
1969b *Gosavia humberti*; Iqbal, p. 55, pl. 5, fig. 77.
1972 *Gosavia humberti*; Iqbal, p. 65, pl. 16, fig. 5.
1978 *Indovoluta humberti*; Bhatia and Khosla, p. 246, pl. 4, fig. 11.

Lectotype.—GSL 9886, lower Eocene, Sindh, Pakistan.

Occurrence.—Paleocene to middle Eocene, several areas of Pakistan; upper Eocene, Myanmar; middle Eocene, Subathu Formation, Himachal Pradesh, India; lower Eocene, Khuiala Formation, Rajasthan, India; lower Eocene, Naredi Formation and middle Eocene, Harudi Formation, Kutch, India.

Description.—Biconic, large (largest specimen 81 mm height, 51.5 mm diameter), moderately wide; spire barely elevated only near apex; protoconch bulbous, approximately one whorl; teleoconch ~ 5 whorls; whorl side only slightly convex at posterior part, flat conical anteriorly. Anterior end of columella slightly bent; suture on internal mold marked by prominent gap between whorls, flushed with surface where shell preserved; shoulder rounded on internal mold, nearly angular with shell. Shelf very slightly inclined, slightly depressed near shoulder; aperture narrow, elongated, parallel-sided, almost rectangular with distinct siphonal notch; latest ontogeny marked by slight flaring of aperture and upturned suture in internal mold; inner lip characterized by distinct thin parietal callus and prominent columellar plaits, plaits stronger and closer in anterior part, relatively more distantly spaced posteriorly, generally eight or nine columellar plaits, sometimes with fainter intermediary plaits at different ontogenetic stages; surface smooth; growth lines with prominent asymmetric flexure on shelf, straight on whorl side, sharply flexed in anterior part in connection with siphonal notch; siphonal fasciole not demarcated by any border. Shell moderately thick, thicker on shelf, characteristically draping approximately half of shelf of previous whorl; basal constriction weak; faint basal grooves posterior to anterior siphonal flexure.

Materials.—Twenty-four specimens: one (PG/KG/Vl 2) from the Naredi Formation at Loc. 1; others from the Harudi Formation, 11 (PG/KG/Vl 7, 16–24, 123) from Loc. 2, seven (PG/KG/Vl 8, 9, 11–15) from Loc. 3, and five (PG/KG/Vl 1, 3–6) from Loc. 4. Majority of specimens adult to subadult.

Remarks.—*Indovoluta humberti* was known so far mainly from different areas of Pakistan. It was also recorded from Himachal Pradesh and Rajasthan of India. It ranges in age from the Paleocene to the middle Eocene (d'Archiac and Haime, 1854; Cox, 1931; Vokes, 1937; Eames, 1952; Iqbal, 1969b, 1972; Bhatia and Khosla, 1978). However, the only formal description of the species was by d'Archiac and Haime (1854). The present report extends the distribution of the species further south to Kutch. We redescribe the species, adding new information regarding shell morphologies, e.g., partial draping of the shelf by succeeding whorls (Fig. 4.7). D'Archiac and Haime (1854) mentioned the presence of 15 or 16 columellar plaits in the inner lip. On the other hand, Cox (1931) and Eames (1956) found 5–7 plaits. The number of columellar plaits in Kutch specimens is generally 8 or 9, sometimes with several associated intercalatories.

Indovoluta multidentata (d'Archiac and Haime, 1854)

Figure 5.1–5.8

1854 *Voluta multidentata* d'Archiac and Haime, p. 326, pl. 32, fig. 1.
1931 *Gosavia multidentata*; Cox, p. 58.
1937 *Gosavia multidentata*; Vokes, p. 7.
1952 *Gosavia multidentata*; Eames, p. 114.
1956 *Indovoluta multidentata*; Eames, p. 109.

Lectotype.—GSL 9885, lower Eocene, Sindh, Pakistan.

Occurrence.—Paleocene to middle Eocene, several areas of Pakistan; middle Eocene, Subathu Formation, Himachal Pradesh and Harudi Formation, Kutch, India.

Description.—Biconic, small (largest specimen 48.5 mm height, 18 mm diameter), narrow, thick-shelled; spire moderately raised; protoconch bulbous, of approximately one whorl; teleoconch ~ 4 whorls; whorl side slightly convex toward posterior, flat conical toward anterior; shelf narrow, slightly sloping, depressed, bordered by sharp, angular, slightly elevated shoulder; suture prominent, lying just below shoulder; in internal mold shoulder not demarcated and suture prominently impressed; columella slightly bent at anterior part; eight or nine prominent columellar plaits characterizing inner lip, with anterior plaits relatively stronger than posterior plaits; sometimes weaker plaits, five or six in number, alternate with stronger ones in later ontogeny; parietal callus prominent, relatively thick in posterior part; aperture narrow subrectangular, high narrow in posterior end, relatively wider in anterior end; siphonal notch shallow; growth lines with slightly asymmetric distinct subsutural flexure on shelf, convex forward at posterior end of whorl, becoming straight later, unknown at anterior part; adult aperture flared or thickened internally, with suture slightly upturned in internal mold; base only slightly constricted.

Materials.—Forty-seven specimens, all from the Harudi Formation: 14 (PG/KG/Vl 65–75, 107–109) from Loc. 2, 29 (PG/KG/Vl 76–102, 110, 111) from Loc. 3, and four (PG/KG/Vl 103–106) from Loc. 4; mostly internal molds, shell preserved in some parts.

Remarks.—*Indovoluta multidentata* has been reported from the Paleocene and the middle Eocene of different parts of Pakistan, and Himachal Pradesh, India (d'Archiac and Haime, 1854; Vredenburg, 1923; Douvillé, 1929; Vokes, 1937; Eames, 1952, 1956). This is the first report of the species from the middle Eocene of Kutch. The species was primarily distinguished from contemporaneous *Indovoluta humberti* in having a smaller, narrower shell, with less conical whorls, more convex sides, and a higher number of columellar plaits (Cox, 1931; Eames, 1956). We found similarity in number of columellar plaits between these two species. However, its smaller size, narrower shell outline, more elevated spire, and sharper raised shoulder easily distinguish *Indovoluta multidentata* from other congeneric species. In *Indovoluta multidentata*, the suture lies just below the shoulder, whereas in *Indovoluta humberti*, it overrides the preceding shelf.

Genus *Involuta* Cox, 1931

Type species.—*Involuta daviesi* Cox, 1931, middle Eocene, Pakistan, by monotypy.

Involuta daviesi Cox, 1931
Figure 5.9–5.21

1931 *Involuta daviesi* Cox, p. 58, pl. 2, figs. 2, 4.
1937 cf. *Involuta daviesi*; Vokes, p. 7.
1952 *Involuta daviesi*; Eames, p. 115.

Holotype.—NHM G.50161, middle Eocene, Balochistan, Pakistan.

Occurrence.—Middle Eocene, different areas of Pakistan; middle Eocene, Subathu Formation in Himachal Pradesh, and Harudi Formation in Kutch, India.

Description.—Large (largest measures ~ 165 mm height, 100 mm diameter), prominently involute with deep umbilicus on apical side, ovate-conical; protoconch paucispiral, slightly greater than one whorl, bulbous, smooth; teleoconch of ~ 4 whorls; whorl side convex on posterior part, conical in anterior part; shoulder angular; shelf wide, convex, adaxially inclined; sutures deeply impressed; aperture narrow, crescentic, parallel-sided; ~ 15 more or less regularly arranged columellar plaits, strength of plaits decreasing whereas spacing slightly increasing posteriorly; basal constriction weak; columella only slightly curved; shell thin, relatively thickened toward posterior; growth lines with shallow subsutural flexure close to shoulder, straight on whorl side, with flexure on anterior part for siphonal notch; siphonal fasciole not observed except for faint groove demarcating posterior end of anterior flexure in some specimens; shell surface essentially smooth, except more or less regularly arranged, well-spaced, collabral, sharp striae and faint spiral undulations, in early ontogeny weak reticulation on posterior part.

Materials.—Nine specimens, all from the Harudi Formation: four (PG/KG/Vl 25, 26, 120, 121) from Loc. 2, five (PG/KG/Vl 27-31) from Loc. 3; all internal molds, with shell preserved at some parts.

Remarks.—This is only the second report of the genus from India. The species was so far known from Pakistan (Cox, 1931; Eames, 1952), and the Subathu Formation from Himachal Pradesh, India (Vokes, 1937). The specimens reported here from Kutch resemble the species closely and are considered conspecific. Their size and shape, involute nature with a deep apical umbilicus, their narrow, parallel-sided, crescentic apertures, and the number and pattern of columellar plaits match very closely. The only other species referred here to this genus is much smaller and is discussed below.

Involuta coxi new species
Figure 6.1–6.7

Holotype.—PG/KG/Vl 42, from the Harudi Formation exposed at Loc. 3; internal mold.

Diagnosis.—Small, convolute; shelf narrow, flat, horizontal; shoulder weak.

Occurrence.—Middle Eocene Harudi Formation, Kutch, Gujarat, India.

Description.—Small (largest 47.5 mm height, 26 mm diameter), convolute, ovate-conical; protoconch paucispiral, slightly greater than one whorl, bulbous, smooth; teleoconch < 3 whorls; whorl side rounded toward posterior, conical anteriorly; suture impressed; aperture narrow, slightly wide anteriorly, posteriorly curved and almost straight in anterior part; shelf narrow, horizontal; shoulder rounded, not prominent; ~ 15 more or less regularly arranged columellar plaits, stronger and more closely spaced toward anterior; basal constriction weak; columella only slightly curved; shell thin; growth lines straight on whorl side, unknown on shelf and anterior end; suture at latest ontogeny slightly upturned along with slightly constricted labrum in internal mold.

Etymology.—In honor of L.R. Cox, who did pioneering studies on mollusks from the Indian subcontinent.

Materials.—Sixteen specimens, all from the Harudi Formation: seven (PG/KG/Vl 32–38) from Loc. 2, six (PG/KG/Vl 42, 43, 116–119) from Loc. 3, and three (PG/KG/Vl 39–41) from Loc. 4; seven designated paratypes PG/KG/Vl 32, 34, 37, 43, 117–119; PG/KG/Vl 32 with partially preserved shell, others internal molds.

Remarks.—The species is easily distinguishable from *Involuta daviesi* in two respects—size and coiling pattern. It is much smaller than the latter species. Adult size in a volutid gastropod, which is characterized by indeterminate growth, can only be surmised from the large individuals of a population. In case of *Involuta coxi* n. sp., however, the upturned suture along with the constricted aperture perhaps indicate that it was approaching adulthood. However, this dwarf species is easily distinguished from its larger sister by its coiling pattern—*Involuta coxi* n. sp. is convolute whereas *Involuta daviesi* is strongly involute with apical umbilicus. The apical umbilicus is already evident in the very first teleoconch whorl of the latter (Fig. 5.16). Shoulder and shelf, which are very well developed in *Involuta daviesi*, are not prominent in *Involuta coxi* n. sp. The aperture with a slight widening toward the anterior end in *Involuta coxi* n. sp. also differs from that in *Involuta daviesi*. However, the overall ovate-conical shape and the number and nature of the columellar plaits are similar in the two species.

Subfamily Athletinae Pilsbry and Olsson, 1954
Genus *Athleta* Conrad, 1853
Subgenus *Volutocorbis* Dall, 1890

Type species.—*Volutilithes limopsis* Conrad, 1860, Paleocene, USA, by original designation.

Remarks.—*Volutocorbis* was synonymized with *Athleta* by Darragh (1971). Merle et al. (2014), however, rightly pointed out that this and some other morphotypes of *Athleta* are still recognizable primarily because of their characteristic ornamentation. *Volutocorbis* with spiral rows of tubercles arranged on collabral ribs on the whorl side is easily distinguishable from other members of the genus *Athleta*. We uphold the view of Merle et al. (2014) and use *Volutocorbis* as a subgenus.

Several similar looking species of *Volutocorbis* have been recorded from the Paleocene-Eocene strata of Pakistan. They resemble one another in an ornamental pattern in which tubercles are arranged in a reticulate fashion. The tubercles are roughly equidimensional and spaced equidistantly. They are slightly upturned to produce a rasp-like appearance. Species are differentiated based mainly on shell size and morphometric proportions, and the relative spacing of the spiral and axial components of the ornaments. For instance, *Volutocorbis eugeniae* Vredenburg, 1923, with which *Volutospina sykesi* (d'Archiac and Haime, 1854) (sensu Cossmann and Pissarro, 1909) was synonymized by Merle et al. (2014), is large and slender and has four spiral rows of tubercles on the spire whorls. *Volutocorbis burtoni* Vredenburg, 1923, which subsumes *Volutocorbis victoriae* Vredenburg, 1923 and *Volutocorbis soriensis* Eames, 1952 (Merle et al., 2014), is slightly stouter and has two or three spiral rows of tubercles on the spire whorls. These characters, however, appear to vary intraspecifically and also ontogenetically. For example, in *Volutocorbis daviesi* Cox, 1930, spiral rows of tubercles are reduced from four on early whorls to three on the penultimate whorl (Cox, 1930). These varieties, however, are often found to be geographically and stratigraphically restricted and mutually exclusive. Hence, their specific identity is justified.

In other recorded species of *Volutocorbis* from Pakistan, either the axial or the spiral component is dominant. They are also distinguished based on similar minor morphological differences. These morphological variants, again, have restricted and often nonoverlapping geographic and temporal ranges.

Athleta (*Volutocorbis*) *harnaiensis* Cox, 1931
Figure 6.8–6.15

1931 *Volutocorbis harnaiensis* Cox, p. 56, pl. 2, fig. 7.
1969a *Volutocorbis harnaiensis*; Iqbal, p. 23, pl. 10, figs. 3–4.

Holotype.—NHM G.50111, lower Eocene, Balochistan, Pakistan.

Occurrence.—Lower Eocene, Balochistan, Pakistan; middle Eocene, Harudi Formation, Kutch, India.

Description.—Small (largest 21.5 mm height, 10.5 mm diameter), biconic-fusiform; spire low; last whorl much larger; protoconch not fully preserved, small; four spire whorls, ~ 20% of each exposed; whorls convex; suture impressed where shell preserved, marked by distinct gap in internal mold; basal constriction very prominent; aperture narrow, elliptical, slightly widening anteriorly; inner lip with parietal callus and four prominent columellar plaits; surface of internal mold marked by series of spiral grooves on entire whorl side posterior to basal constriction; grooves closer anteriorly; preserved shell surface ornamented with closely spaced tubercles in reticulate arrangement; posteriormost row of tubercles somewhat separated from remaining, forming shoulder-like angulation; collabral growth lines essentially straight on whorl side, tending to bend back at basal extremity for shallow siphonal notch.

Materials.—Twenty-one specimens, all from the Harudi Formation: five (PG/KG/Vl 52-54, 113, 122) from Loc. 2, nine (PG/KG/Vl 55-61, 114, 115) from Loc. 3, and seven (PG/KG/Vl 45-51) from Loc. 4; mostly internal molds, a few with well-preserved shells.

Remarks.—The specimens from Kutch resemble *Volutocorbis harnaiensis* very closely except in having a slightly smaller shell. On the spire whorls, four rows of spiral tubercles are visible, whereas 18 or 19 are found on the last whorl. On the last whorl, 27 axial costae are observed. This count falls within the wide range recorded by Cox (1931) for the species from Pakistan. *Volutocorbis eugeniae* has a similar number of visible spiral rows on the spire whorls and axial costae on the last whorl but is larger and relatively slender. *Volutocorbis daviesi* also differs from *Volutocorbis harnaiensis* in minor ornamental details and is slenderer. This is the first report of this species from Kutch.

Subfamily Volutinae Rafinesque, 1815
Tribe Lyriini Pilsbry and Olsson, 1954
Genus *Lyria* Gray, 1847

Type species.—*Voluta nucleus* Lamarck, 1811, Recent, eastern Australia, by original designation.

Lyria? cf. *Lyria punjabensis* Eames, 1952
Figure 6.16–6.18

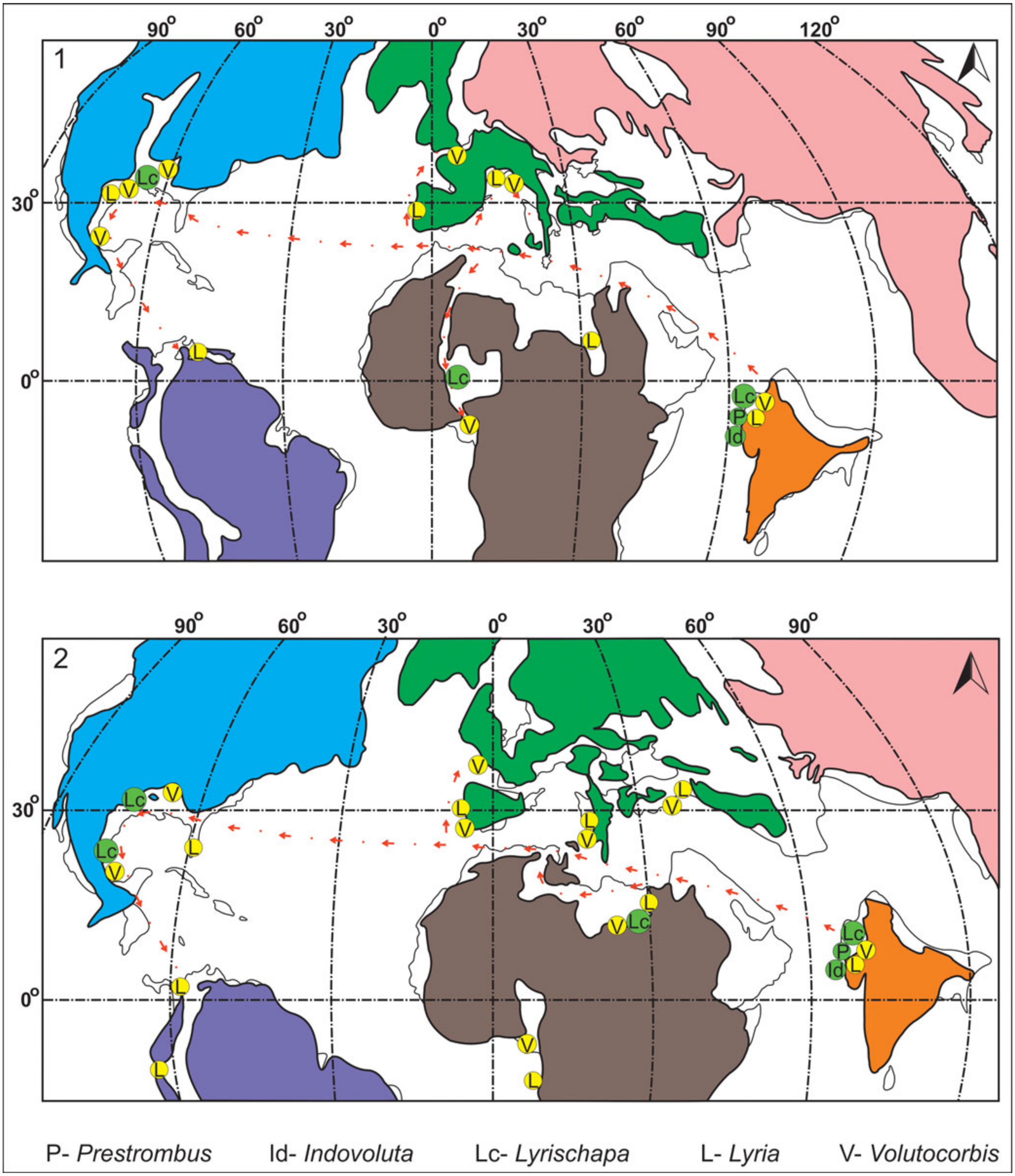


Figure 7. Paleobiogeographic distribution of indovolutine and other volutid genera discussed herein during the Paleocene (**1**) and the lower Eocene (**2**). Suggested routes of larval dispersal marked by arrows. Paleocoastline maps modified after Smith et al. (1994).

1952 *Lyria punjabensis* Eames, p. 107, pl. 4, fig. 92.
1969b *Lyria* cf. *Lyria punjabensis* (?); Iqbal, p. 56, pl. 6, fig. 78.

Holotype.—NHM G.68306, middle Eocene, western Punjab, Pakistan.

Occurrence.—Middle Eocene, Pakistan; doubtfully also from Paleocene, Pakistan; middle Eocene, Harudi Formation, Kutch, India.

Description.—Small (26 mm height, 14 mm diameter), lyriform; protoconch paucispiral, small, bulbous, ~1–1.5

whorl, ~2.5 mm diameter, protoconch boundary not well-marked; teleoconch ~3.5 whorls; spire moderately raised; suture moderately impressed; spire whorls slightly convex; last whorl rounded posteriorly, becoming straight from middle to base; aperture subelliptical with shallow siphonal notch; prominent callus on inner lip; prominent axial costae throughout shell surface, with 14 costae on each whorl; costae becoming finer and closely spaced on latest part of last whorl; growth lines only slightly convex at posterior end, straight on whorl side, curving backward at base, paralleling siphonal notch; siphonal fasciole absent.

Material.—One specimen (PG/KG/Vl 44) from the Harudi Formation exposed at Loc. 4, with preserved shell.

Remarks.—The only specimen in our collection is comparable to *Lyria punjabensis* in most respects. Costae are prominent and widely spaced in both. However, the Kutch form differs from *Lyria punjabensis* in having finer and more closely spaced costae in the latest part of the last whorl. The generic status of the form is also doubtful because in a typical *Lyria*, the spire is higher and there are two or three strong columellar plaits on the basal part of the inner lip. The present species does not have an elevated spire. Columellar plaits cannot be studied due to the presence of matrix on the inner lip. Eames (1952) also could not observe collumellar plaits, however, he assigned it to the genus *Lyria*. It resembles the genus *Lyriopsis* Merle et al., 2014 due to the presence of a shorter spire. However, the absence of a shoulder and the curvature of the costae at the posterior end distinguish it from *Lyriopsis*.

Discussion

Paleobiogeography.—The subfamily Indovolutinae n. subfam. apparently evolved and flourished in the western part of the Indian subcontinent. *Indovoluta* was known from Sindh Province of Pakistan, and Himachal Pradesh and Rajasthan in India (d'Archiac and Haime, 1854; Cox, 1931; Vokes, 1937; Eames, 1952; Iqbal, 1969b, 1972; Bhatia and Khosla, 1978). *Involuta* was restricted to the western part of the Indian subcontinent and known from Pakistan and Himachal Pradesh (Cox, 1931; Vokes, 1937; Eames, 1952). *Prestrombus* was known only from Pakistan and Rajasthan (Cox, 1931; Eames, 1952; Bhatia and Khosla, 1978). Whereas these genera of this subfamily were largely restricted to this Tethyan province, *Lyrischapa* appears to have migrated to America. The latter speciated there during the lower and middle Eocene. This genus is also known from the Eocene of Egypt (Abbass, 1967) and Mexico (Perrilliat et al., 2006) and the Paleocene of Niger (Givens, 1991). Givens (1991) thought that some kind of sweepstake mechanism was involved in the migration of *Lyrischapa* from the Tethyan part to the USA because it lacked planktotrophic larval ontogeny. The presence of the westward-flowing Tethys Paleocurrent (Haq, 1981) and perhaps also volcanic islands on the way from east to west facilitated this transatlantic dispersal (Givens, 1991). However, the absence of *Lyrischapa* in most of the Mediterranean basins, especially those in the southern part of Europe, is noteworthy. Southern European basins are known to yield the most diverse gastropod fauna of the Paleogene (Das and Halder, 2016, 2018). It appears that the genus evolved in the western Indian province during the Paleocene and migrated along the southern border of the relict Tethys Sea before crossing over to the western shores of the Atlantic (Fig. 7). Harzhauser et al. (2002), following Popov (1993), demonstrated an eastward current along northern shores of the relict Tethys and a westward current along its southern shores during the upper Eocene (Harzhauser et al., 2002, fig. 3). The above scenario of dispersal of *Lyrischapa* appears to be plausible if there were similar currents operative during earlier parts of the Paleogene.

Givens (1989) reported the presence of several more Tethyan faunal components in the Gulf Coastal Plain. He recorded 32 gastropod and 14 bivalve genera that migrated from the Tethys Realm to the USA. A recent analysis involving all Paleocene and Eocene gastropod genera recorded in the "Compendium" (Sepkoski, 2002) and their geographic distribution data as obtained from the Paleobiology Database (http://fossilworks.org/) reveals very high generic similarity across the Atlantic between the Mediterranean and the eastern American basins (Das and Halder, 2016, 2018). Out of 252 Eocene gastropod genera from the Gulf Coastal Plain, 119 are also known from the Mediterranean basins. In the Paleocene, this ratio was 51 out of 136. Both of these provinces also exhibit high generic similarity with Central American and Caribbean basins (Das and Halder, 2016, 2018).

A distribution pattern somewhat similar to that shown by *Lyrischapa*, conspicuous by its absence or poor representation in the middle of its distribution, has also been exhibited by some other groups of mollusks. They are abundant and diverse in the eastern part of the Tethys Realm represented by the western Indian basins (Western Indian Province, sensu Harzhauser, 2007) and in the western Atlantic provinces of the Gulf Coastal Plain, and Central American and Caribbean basins. *Kapalmerella* Allmon, 2005 (= *Palmerella* Allmon, 1996), which belongs to the gastropod family Turritellidae Lovén, 1847, is known extensively from the USA. It has recently been reported from Kutch (Halder and Sinha, 2014). *Turritella ranikoti* Vredenburg, 1928b, known from Pakistan and now also from Kutch, has been reassigned to this genus (Halder and Sinha, 2014). Except in Egypt, this genus has not been reported from the western part of the Tethys Realm, i.e., the Mediterranean basins (Mediterranean Iranian Province, sensu Harzhauser et al., 2002). *Glyptoactis* Stewart, 1930, a bivalve belonging to the family Carditidae Férussac, 1822, was also quite diverse in the USA and western India (d'Archiac and Haime, 1854; Vokes, 1937; Tandon, 1971; Mathur, 1975; Bhatia and Khosla, 1978; Halder, unpublished data) but much less so in the Mediterranean Iranian Province. Haas and Miller (1952) also found maximum similarity of the Eocene nautiloid (Nautiloidea Agassiz, 1847, Cephalopoda Cuvier, 1797) fauna from America with that of Pakistan.

Emaciated presence of certain genera in the middle of their distribution in the Mediterranean and Middle East countries is, however, an exception rather than the rule. The Western Indian Province shares much with these areas. Out of 87 Eocene gastropod genera that were reported in the "Compendium" (Sepkoski,

2002) and known from the western Indian basins (http://fossilworks.org/), 67 are also known from the Mediterranean Iranian Province. The Western Indian Province fauna displays relatively less similarity with the Gulf Coastal Plain fauna. They have 53 gastropod genera in common during the Eocene whereas the Western Indian Province had a total of 87 and the Gulf Coastal Plain 252 known genera (Sepkoski, 2002).

Das and Halder (2016, 2018) demonstrated that in the Paleogene a broadly similar gastropod fauna lived in the circumtropical and subtropical zones including those mentioned above and western American basins such as California, Oregon, and Washington, and Southeast Asia (viz. mainly Indonesia). A strongly different fauna existed in the contemporaneous basins of Australia and New Zealand. This distribution pattern indicates strong influence of temperature and wide dispersibility of many gastropods, and also the presence of dispersal routes and favorable currents. Indovolutinae n. subfam. was an atypical representative of this widespread fauna having abundance only in the western part of the Indian subcontinent and America.

In contrast to Indovolutinae n. subfam., the two other volutid genera reported here have a wide geographic distribution in different Tethyan basins and North America during the lower Paleogene. The oldest representatives of *Athleta* come from the Upper Cretaceous of Egypt (Kassab et al., 1995) and Poland (Abdel-Gawad, 1986). The oldest representative of the morphotype *Volutocorbis* Dall, 1890 also comes from the Upper Cretaceous of Egypt (Kassab et al., 1995). It appears, therefore, that this volutid is also essentially a Tethyan form that crossed the Atlantic in the lower Paleogene (Fig. 7). In the Paleogene, *Athleta* was most widespread and present in Southeast Asia as far south as Australia and New Zealand (Maxwell, 2003). The genus survives today in a relatively restricted geographic occurrence in Africa, Australia, and New Zealand (Maxwell, 2003 and references therein). The earliest *Lyria* spp. were also recorded from the Upper Cretaceous Tethyan basins of Central Asia (Pojarkova, 1984) and the United Arab Emirates (Gameil, 2005). Later, it flourished through a large part of the Tethys Realm in the Paleogene and crossed over to America in the Paleocene (Darragh, 1989; http://fossilworks.org/) (Fig. 7). Its distribution widened in the Neogene to several of the western Pacific and Australian basins. It is survived today by several species distributed in western Atlantic and western Pacific countries, and Australia (Maxwell, 2003 and references therein).

Remarks.—The Paleogene members of the subfamily Indovolutinae n. subfam. had nonplanktotrophic development; all of them are characterized by paucispiral, bulbous protoconchs. All but *Lyrischapa* were geographically very restricted and had low specific diversity. *Lyrischapa* appears to have speciated rapidly by allopatry after fortuitous dispersals by sweepstake routes despite having nonplanktotrophic larvae (Hansen, 1982). The subfamily did not live long and was restricted to the Paleocene and the Eocene after its origin in the Cretaceous with *Gosavia.* Evolution of this subfamily demonstrates the close link of nonplanktotrophic development and restricted geographic distribution with low specific diversity and extinction.

Modern volutids have lecithotrophic development (Bouchet and Poppe, 1988), which is reflected in their narrow geographic ranges. *Athleta* and *Lyria* are two exceptions that managed to disperse widely in the past, especially in the Paleogene. The wide geographic distribution of *Athleta* in the Paleogene has been attributed to larval planktotrophy (Fischer et al., 1964; Darragh, 1971, 1989; Hansen, 1978, 1982). Later, by the Neogene, planktotrophy was suppressed in all volutes (Bouchet and Poppe, 1988) including members of Athletinae. *Volutocorbis* spp., with conical multispiral protoconchs in the Paleogene (Merle et al., 2014), had planktotrophic development (Hansen, 1982) and expectedly achieved wide geographic distribution. This morphotype of *Athleta* survives today.

The *Lyria* species reported here had lecithotrophic development. However, the genus was known also by planktotrophic development (Maxwell, 2003). Modern species of the genus are known by large, bulbous protoconchs reflecting nonplanktotrophic development, but some show disjunct populations separated by deep ocean basins. This observation led to different explanations, e.g., the presence of a demersal swimming larval stage (Bouchet and Poppe, 1988; Bouchet and Bail, 1991) and polyphyletic origin from species with planktotrophic larval ontogeny (Maxwell, 2003). The wide geographic and temporal distributions and large specific diversity of the genus is perhaps due to its diverse developmental strategy.

Acknowledgments

We are thankful to an anonymous reviewer and D. Friend for providing valuable suggestions. We thank the Director and staff of the Curatorial Division, Repository of Fossils, Geological Survey of India, Kolkata for providing permission and logistic support to study type specimens. The study was financially supported by Science and Engineering Research Board, Department of Science and Technology, India (Project nos. SR/S4/ES/653-2012 and EMR/2016/002583), and the FRPDF scheme of Presidency University.

References

Abbass, H.L., 1967, A monograph on the Egyptian Paleocene and Eocene gastropods: United Arab Republic Geological Survey, Geological Museum, Palaeontological Series, Monograph 4, 154 p.

Abdel-Gawad, G.I., 1986, Maastrichtian non-cephalopod mollusks: Scaphopoda, Gastropoda and Bivalvia of the Middle Vistula Valley, central Poland: Acta Geologica Polonica, v. 36, p. 69–224.

Agassiz, L., 1847, Lettre sur quelques points de'organisation des animaux rayonnes: Paris Comptes Rendus, v. 25, p. 677–682.

Aldrich, T.H., 1911, New Eocene fossils from the southern Gulf states: Bulletins of American Paleontology, v. 5, p. 1–24.

Allmon, W.D., 1996, Systematics and evolution of Cenozoic American Turritellidae (Mollusca: Gastropoda) I: Paleocene and Eocene Coastal Plain species related to "*Turritella mortoni* Conrad" and "*Turritella humerosa* Conrad": Palaeontographica Americana, no. 59, p. 1–134.

Allmon, W.D., 2005, *Kapalmerella*, a new name for the genus *Palmerella* Allmon, 1996 (Gastropoda: Turritellidae) preoccupied by *Palmerella* Cameron, 1908 (Insecta: Hymenoptera): Journal of Paleontology, v. 79, p. 1234, doi:10.1666/0022-3360(2005)079[1234:KANNFT]2.0.CO;2.

Bhatia, S.B., and Khosla, S.C., 1978, Some lower Eocene Mollusca from Rajasthan: Recent Researches in Geology, v. 4, p. 225–249.

Biswas, S.K., 1992, Tertiary Stratigraphy of Kutch: Journal of the Palaeontological Society of India, v. 37, p. 1–29.

Bouchet, P., and Bail, P., 1991, Volutes from Saya de Malha Bank: The saga *of Lyria surinamensis* and a new species: The Nautilus, v. 105, p. 159–164.

Bouchet, P., and Poppe, G.T., 1988, Deep water volutes from the New Caledonian region, with a discussion on biogeography: Venus, The Japanese Journal of Malacology, v. 47, p. 15–32.

Bouchet, P., Kantor, Y.I., Sysoev, A., and Puillandre, N., 2011, A new operational classification of the Conoidea (Gastropoda): Journal of Molluscan Studies, v. 77, p. 273–308, doi:10.1093/mollus/eyr017.

Catuneanu, O., and Dave, A., 2017, Cenozoic sequence stratigraphy of the Kachchh Basin, India: Marine and Petroleum Geology, v. 86, p. 1106–1132, doi:10.1016/j.marpetgeo.2017.07.020.

Conrad, T.A., 1853, Synopsis of the genera *Cassidula*, Humph., and of a proposed new genus *Athleta*: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 6, p. 448–449.

Conrad, T.A., 1860, Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama: Journal of the Academy of Natural Sciences of Philadelphia, ser. 2, v. 4, p. 275–298.

Cossmann, M., and Pissarro, G., 1909, The Mollusca of the Ranikot Series, Part 1, Cephalopoda and Gastropoda: Palaeontologia Indica, n. ser. 3, no. 1, p. 1–83.

Cox, L.R., 1930, The fossil fauna of the Samana Range and some neighbouring areas, Part 8, The Mollusca of the Hangu Shale: Memoirs of the Geological Survey of India, Palaeontologia Indica, n. ser., v. 15, p. 129–222.

Cox, L.R., 1931, A contribution to the molluscan fauna of the Laki and basal Kirthar groups of the Indian Eocene: Transactions of the Royal Society of Edinburg, v. 57, part 1, no. 2, p. 25–92.

Cox, L.R., 1960, General characteristics of Gastropoda, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part I, Mollusca 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. I84–I169.

Cuvier, G., 1797, Tableau Elementaire d'Histoire Naturelle des Animaux: Paris, 710 p.

Dall, W.H., 1890, Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene Silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River: Transactions of the Wagner Free Institute of Science, v. 3, p. 1–200.

Dalton, L.V., 1908, Notes on the geology of Burma: The Quarterly Journal of the Geological Society of London, v. 64, p. 604–644.

d'Archiac, A.S., and Haime, J., 1854, Description des Animaux Fossiles du Groupe Nummulitique de l'Inde, Seconde Livraison: Mollusques: Paris, Gide et J. Baudry, p. 225–373.

d'Orbigny, A.D., 1839, Foraminifères, *in* Sagra, R. de la M., Histoire Physique, Politique et Naturelle de l'Ile de Cuba: Paris, Arthus Bertrand, 336 p.

Darragh, T.A., 1971, Revision of the Australian Tertiary Volutidae (Mollusca: Gasteropoda), 1, The subfamily Athletinae: Journal of the Malacological Society of Australia, v. 2, p. 163–185.

Darragh, T.A., 1989, A revision of the Tertiary Volutidae (Mollusca: Gastropoda) of south-eastern Australia: Memoirs of the Museum of Victoria, v. 49, p. 195–307.

Das, S., and Halder, K., 2016, Early Paleogene gastropod distribution had Tethyan influence and circum-tropical distribution: Developments in Geosciences in the Past Decade—Emerging Trends for the Future & Impact on Society, Abstracts, p. 154–155.

Das, S., and Halder, K., 2018, Control of climate and Tethyan legacy on distribution of Paleocene–Eocene gastropods and establishment of the Northern Tropical Realm: Journal of Earth System Science, v. 127, art. 58, p. e58, doi:10.1007/s12040-018-0959-7.

Douvillé, H., 1920, L'Eocène au Soudan et au Sénégal: Bulletin du Comite d'Études Historiques et Scientifiques de l'Afrique Occidentale Francaise, p. 113–170.

Douvillé, H., 1929, Les couches à *Cardita beaumonti* dans le Sind: Memoirs of the Geological Survey of India, Palaeontologia Indica, n. ser., v. 10, p. 27–73.

Eames, F.E., 1952, A contribution to the study of the Eocene in western Pakistan and western India, C, The description of the Scaphopoda and Gastropoda from standard sections in the Rakhi Nala and Zinda Pir areas of the western Punjab and in the Kohat District: Philosophical Transactions of the Royal Society of London, B, Biological Sciences, v. 236, no. 631, p. 1–168.

Eames, F.E., 1956, *Indovoluta*, a new Eocene volutid genus: Proceedings of the Malacological Society of London, v. 32, p. 109.

Férussac, A.E., 1821–1822, Tableaux Systématiques des Animaux Mollusques Classés en Familles Naturelles, dans Lesquels on a Établi la Concordance de Tous les Systèmes: Suivis d'un Prodrome Général pour Tous les Mollusques Terrestres ou Fluviatiles, Vivants ou Fossils: Paris, Arthus Bertrand, 111 p.

Fischer, W.L., Rodda, P.U., and Dietrich, J.W., 1964, Evolution of *Athleta petrosa* stock (Eocene, Gastropoda) of Texas: Bureau of Economic Geology, University of Texas Publication 6413, 117 p.

Fleming, J., 1822, The Philosophy of Zoology or a General View of the Structure, Functions, and Classification of Animals, Volume 2: Edinburgh, Archibald Constable & Company, 618 p.

Gameil, M., 2005, Palaeoecological implications of Upper Cretaceous solitary corals, United Arab Emirates/Oman borders: Revue de Paleobiologie, v. 24, p. 515–532.

Givens, C.R., 1979, The gastropod genus *Volutocristata* Gardner and Bowles (Eocene, California, Mexico): A synonym of *Lyrischapa* Aldrich (Eocene, Gulf Coast): Tulane Studies in Geology and Paleontology, v. 15, p. 117–128.

Givens, C.R., 1989, First record of the Tethyan genus *Volutilithes* (Gastropoda: Volutidae) in the Paleogene of the Gulf Coastal Plain, with a discussion of Tethyan molluscan assemblages in the Gulf Coastal Plain and Florida: Journal of Paleontology, v. 63, p. 852–856.

Givens, C.R., 1991, Old world Tethyan occurrences of *Lyrischapa* (Gastropoda; Volutidae) and biogeographic implications: Journal of Paleontology, v. 65, p. 661–670.

Gümbel, C.W. von, 1868, Beiträge zur Foraminiferenfauna der Nordalpinen, älteren Eocängebilde oder der Kressenberger Nummulitenschichten: Abhandlungen der Mathematisch-Physikalischen Klasse der Königlich Bayerischen Akademie der Wissenschaften, v. 10, pt. 2, p. 579–730.

Gray, J.E., 1847, A list of the genera of Recent Mollusca, their synonyms and types: Proceedings of the Zoological Society of London, v. 15, p. 129–219.

Haas, O., and Miller, A.K., 1952, Eocene nautiloids of British Somaliland: Bulletin of the American Museum of Natural History, v. 99, p. 313–354.

Halder, K., 2012, Cenozoic fossil nautiloids (Cephalopoda) from Kutch, western India: Palaeoworld, v. 21, p. 116–130, doi:10.1016/j.palwor.2012.05.004.

Halder, K., and Bano, S., 2015, Cenozoic Corbulidae (Bivalvia, Mollusca) from the Indian subcontinent—Palaeobiogeography and revision of three species from Kutch, India: Arabian Journal of Geosciences, v. 8, p. 2019–2034, doi:10.1007/s12517-014-1362-6.

Halder, K., and Sinha, P., 2014, Some Eocene cerithioids (Gastropoda, Mollusca) from Kutch, western India, and their bearing on palaeobiogeography of the Indian subcontinent: Paleontology Journal, v. 2014, art. 673469, doi:10.1155/2014/673469.

Hansen, T.A., 1978, Larval dispersal and species longevity in lower Tertiary gastropods: Science, v. 199, p. 885–887.

Hansen, T.A., 1982, Modes of larval development in early Tertiary neogastropods: Paleobiology, v. 8, p. 367–377.

Haq, B.U., 1981, Paleogene paleoceanography: Early Cenozoic oceans revisited, *in* Oceanologica Acta, Proceedings of the 26th International Geological Congress, Geology of Oceans Symposium, Paris 1980, p. 71–82.

Harzhauser, M., 2007, Oligocene and Aquitanian gastropod faunas from the Sultanate of Oman and their biogeographic implications for the early western Indo-Pacific: Palaeontographica, Abt. A, v. 280, p. 75–121.

Harzhauser, M., Piller, W.E., and Steininger, F.F., 2002, Circum-Mediterranean Oligocene-Miocene biogeographic evolution—The gastropods' point of view: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 183, p. 103–133, doi:10.1016/S0031-0182(01)00464-3.

Harzhauser, M., Markus, R., Piller, W.E., Berning, B., Kroh, A., and Mandic, O., 2009, Oligocene and early Miocene gastropods from Kutch (NW India) document an early biogeographic switch from western Tethys to Indo-Pacific: Paläontologische Zeitschrift, v. 83, p. 333–372, doi:10.1007/s12542-009-0025-5.

Iqbal, M.W.A., 1969a, Mega-fauna from the Ghazij Formation (lower Eocene) Quetta Shahrig area, West Pakistan: Memoirs of the Geological Survey of Pakistan, Palaeontologia Pakistanica, v. 5, p. 1–41.

Iqbal, M.W.A., 1969b, The Tertiary pelecypod and gastropod fauna from Drug, Zindapir, Vidor (district D.G. Khan), Jhalar and Chharat (district Campbellpore), West Pakistan: Memoirs of the Geological Survey of Pakistan, Palaeontologia Pakistanica, v. 6, p. 1–95.

Iqbal, M.W.A., 1972, Palaeocene bivalve and gastropod fauna from Jherruk-Lakhra-Bara Nai (Sind), Salt Range (Punjab) and Samana Range (N.W.F.P.), Pakistan: Memoirs of the Geological Survey of Pakistan, Palaeontologia Pakistanica, v. 9, p. 1–105.

Kachhara, R.P., Devi, K.B., and Jodhawat, R.L., 2011a, Molluscan assemblage from the marine Palaeocene sequence in southwestern Kachchh, Gujarat: Journal of the Geological Society of India, v. 78, p. 81–91, doi:10.1007/s12594-011-0061-0.

Kachhara, R.P., Jodhawat, R.L., and Devi, K.B., 2011b, Molluscan biostratigraphy of the Palaeogene sediments around Lakhpat, Kachchh, Gujarat, India: Journal of the Palaeontological Society of India, v. 56, p. 17–28.

Kassab, A., Kenawy, A., and Zakhira, M., 1995, Biostratigraphy of some Upper Cretaceous/lower Tertiary outcrops from the Egyptian Western Desert: Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, v. 196, p. 309–326.

Kulkarni, K.G., Bhattacharjee Kapoor, S., and Borkar, V.D., 2010, Molluscan fauna from the Miocene sediments of Kachchh, Gujarat, India-Part 3: Gastropods: Journal of Earth System Science, v. 119, p. 307–341, doi:10.1007/s12040-010-0026-5.

Lamarck, M., 1811, Sur la détermination des espèces parmi les animaux sans vertèbres, et particulièrement parmi les mollusques testacés: Annales du Muséum National d'Histoire Naturelle, v. 17, p. 54–80.

Landau, B.M. and Marquet, R., 2000, The genus *Cymbium* (Gastropoda, Volutidae) in the Iberian Neogene: Contributions to Tertiary and Quaternary Geology, v. 37, p. 23–34.

Linnaeus, C., 1758, Systema Naturae per Regna Tria Naturae (tenth edition), Volume 1, Regnum Animale: Stockholm, Laurentii Salvii, 824 p.

Lovén, S.L., 1847, Malacozoologii: Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar, v. 4, p. 175–199.

Mathur, N.S., 1975, Mollusca from the Subathu Formation (upper Palaeocene-middle Eocene), Simla Hills: Bulletin, Indian Geologists' Association, v. 8, p. 1–40.

Maxwell, P.A., 2003, The volutid genera *Athleta* and *Lyria* (Mollusca: Gastropoda) in the New Zealand Cenozoic: Journal of the Royal Society of New Zealand, v. 33, p. 363–394, doi:10.1080/03014223.9517735.

Merle, D., Pacaud, J.M., Métais, G., Bartolini, A., Lashari, L.A., Brohi, I.A., Solangi, S.H., Marivaux, L., and Welcomme, J.L., 2014, Volutidae (Mollusca: Gastropoda) of the Lakhra Formation (earliest Eocene, Sindh, Pakistan): Systematics, biostratigraphy and paleobiogeography: Zootaxa, v. 3826, no. 1, p. 101–138, doi:10.11646/zootaxa.3826.1.3.

Milne Edwards, M., 1848, Note sur la classification naturelle des mollusques gastéropodes: Annales des Sciences Naturelles, ser. 3, v. 9, p. 102–112.

Perrilliat, M.D., Avendano, J., Vega, F.J., and Solé, J., 2006, Lower Eocene gastropods from El Bosque Formation, central Chiapas, Mexico: The Veliger, v. 48, p. 151–169.

Pilsbry, H.A., and Olsson, A.A., 1954, Systems of the Volutidae: Bulletins of American Paleontology, v. 35, p. 1–37.

Pojarkova, Z.N., 1984, The Cenomanian and Turonian in northeastern Central Asia: Cretaceous Research, v. 5, p. 1–14.

Ponder, W.F., and Lindberg, D.R., 1997, Towards a phylogeny of gastropod mollusks: An analysis using morphological characters: Zoological Journal of the Linnean Society, v. 119, p. 83–265.

Popov, S.V., 1993, Zoogeography of the late Eocene basins of western Eurasia based on bivalve mollusks: Stratigraphy and Geological Correlation, v. 2, p. 103–118.

Price, R.M., 2001, Using constructional data to detect convergence: An underutilized approach to studying adaptation in the fossil record: Paleobios, v. 21, p. 105–106.

Rafinesque, C.S., 1815, Analyse de la Nature ou Tableau de l'Univers et des Corps Organisés: Palermo, 223 p.

Riedel, F., 2000, Ursprung und Evolution der "höheren" Caenogastropoda: Berliner Geowissenschaftliche Abhandlungen, ser. E, v. 32, p. 1–240.

Röding, P.F., 1798, Museum Boltenianum sive Catalogus Cimeliorum e Tribus Regnis Naturae quae Olim Collegerat Joa. Fried. Bolten: Hamburg, Johan Christi Trapii, 199 p.

Saraswati, P.K., Khanolkar, S., Raju, D.S.N., and Banerjee, S., 2016, An updated Eocene stratigraphy of Kutch: Special Publication of the Geological Society of India, no. 6, p. 25–31, doi:10.17491/cgsi/2016/105406.

Sastry, M.V.A., and Mathur, U.B., 1968, Nautiloid *Aturia* from Eocene of western India: Journal of Paleontology, v. 42, p. 240–242.

Savazzi, E., 1991, Constructional morphology of strombid gastropods: Lethaia, v. 24, p. 311–331.

Sengupta, S., Syed, R., Sarkar, S., and Halder, K., 2011, *Nummulites* Lamarck (Foraminifera) as substrate for other benthonic taxa: A case study from the middle Eocene of western Kutch, Gujarat: Indian Journal of Geosciences, v. 65, p. 265–274.

Sepkoski, J.J., Jr., 2002, A compendium of fossil marine animal genera: Bulletins of American Paleontology, v. 363, p. 5–560.

Smith, M., 1942, A Review of the Volutidae: Winter Park, Florida, Beal-Maltbie Shell Museum, 127 p.

Smith, A.G., Smith, D.G., and Funnel, D.M., 1994, Atlas of Mesozoic and Cenozoic Coastlines: Cambridge, UK, Cambridge University Press, 99 p.

Sowerby, J.C., 1840, Fossils from the Tertiary Formations, Cutch: Transactions of the Geological Society of London, ser. 2, v. 5, pl. 25–26.

Stewart, R.B., 1930, Gabb's California Cretaceous and Tertiary type Lamellibranchs: Special Publication of the Academy of Natural Sciences of Philadelphia, v. 3, p. 1–314.

Stoliczka, F., 1865, Eine revision der Gastropoden der Gosauschichten in den Ostalpen: Sitzungsberichte der Mathematisch-Naturwiessenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, v. 52, p. 104–223.

Swainson, W., 1829–1833, Zoological Illustrations, or Original Figures and Descriptions of New, Rare, or Interesting Animals, Selected Chiefly from the Classes of Ornithology, Entomology, and Conchology, and Arranged According to their Apparent Affinities, Second Series: London, Baldwin and Cradock, (Vol. 1–3): pl. 1–30 (1829), pl. 31–45 (1830), pl. 46–85 (1831), pl. 86–96 (1832), pl. 97–136 (1833).

Swainson, W., 1835, The Elements of Modern Conchology, with Definitions of All the Tribes, Families and Genera, Recent and Fossil, Briefly and Plainly Stated, For the Use of Students and Travelers: London, Baldwin and Cradock, 62 p.

Tandon, K.K., 1971, Occurrence of *Venericardia beaumonti* d'Archiac and Haime from Nareda, south western Kutch, India: Geophytology, v. 1, p. 70–74.

Tandon, K.K., and Srivastava, D.K., 1980, *Hercoglossa kutchensis*—A new species from the middle Eocene rocks of Kutch, India: Journal of the Palaeontological Society of India, v. 23–24, p. 55–57.

Vokes, H.E., 1937, Eocene Mollusca from the Subathu Group (Lutetian) Simla Hill State, India: American Museum Novitates, no. 964, p. 1–13.

Vredenburg, E.W., 1923, Indian Tertiary Gastropoda, IV, Olividae, Harpidae, Marginellidae, Volutidae and Mitridae, with comparative diagnoses of new species: Records of the Geological Survey India, v. 54, p. 243–276.

Vredenburg, E., 1925, Description of Mollusca from the post-Eocene Tertiary formation of north-western India: Cephalopoda, Opisthobranchiata, Siphonostomata: Memoirs of the Geological Survey of India, v. 50, pt. 1, p. 1–350.

Vredenburg, E., 1928a, Description of Mollusca from the post-Eocene Tertiary formation of north-western India: Gastropoda (in part) and Lamellibranchiata: Memoirs of the Geological Survey of India, v. 50, pt. 2, p. 351–506.

Vredenburg, E.W., 1928b, A supplement to the Mollusca of the Ranikot Series: Memoirs of the Geological Survey of India, Palaeontologia Indica, n. ser., v. 10, p. 1–75.

Wenz, W., 1938–1944, Gastropoda, *in* Schindewolf, O.H., ed., Handbuch der Paläozoologie, Volume 6: Berlin, Gebrüder Borntraeger, 1639 p.

Accepted: 23 April 2019