اندوکرینولوژی بالینی زنان ونابارووری اسپیروف

(جلد اول)

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کتاب ارجمند

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پیشگفتار

خیلی خوشحال شدم هنگامی که فهمیدم ویرایش نهم این درس‌نامه قرار است بار دیگر در دانشگاه پِیل چاپ شود. و وقتی که نام خودم را روی جلد دیدم سرشار از حس غرور و قدردانی شدم. چهل و هفت سال پیش بود که باب گلَس و نیتان کِیز از من دعوت کردند که در نوشتن کتابی دربارهٔ ناباروری و اندوکرینولوژی تولید مثل با آنها همکاری کنم. دستنوشته‌های حاصل از آن همکاری یک سال بعد، در ۲۷۳ صفحه و به قیمت ۱۷ دلار به چاپ رسید. پس از آن، هر ویرایش نسبت به ویرایش قبلی گسترده‌تر و آماده کردن ویرایش‌های بعدی دشوارتر شد.

همکاری برای نگارش این کتاب یکی از بهترین و رضایت‌بخش‌ترین تجربه‌های کاری من بوده است. این کتاب درهایی را، نه فقط در کشور خودم که در سرتاسر جهان، به رویم گشود. به خاطر این کتاب بود که من و خانواده‌ام دوستان تازهٔ زیادی پیدا کردیم و به جاهایی سفر کردیم که در رؤیا هم آنها را نمی‌دیدیم. دیدن نشان دانشگاه پِیل روی جلد باعث خرسندی من است. همچنین، دیدن علامت ستارهٔ مقدونیه که از ویرایش ششم به کتاب اضافه شد نیز برایم بسیار جالب است. ستارهٔ مقدونیه نمادی است که به روزگاران گذشته و زمان حکمرانی فیلیپ مقدونی و اسکندر کبیر باز می‌گردد. ای کاش پدربزرگ و مادربزرگم که در سال ۱۹۲۱ از مقدونیه به آمریکا آمدند می توانستند جلد ویرایش نهم را ببینند.

در پیشگفتار ویرایش قبلی، داستانی را گفتم که تکرارش در اینجا خالی از لطف نیست. در سال ۱۹۹۹، کنار خیابانی در شهر نیویورک ایستاده بودم و منتظر بودم که چراغ سبز شود. به دلایل نامعلوم، در آن لحظه فکری به ذهنم خطور کرد که آنچنان قدرتمند بود که مرا سر جایم خشک کرد. در حالی که دیگران با سبز شدن چراغ از خیابان می‌گذشتند من سر جایم ایستاده بودم و با خودم فکر می‌کردم مطالبی که در این کتاب می‌نویسم می‌تواند بر زندگی بیماران تأثیر بگذارد. نیروی این فکر باعث شد عظمت مسئولیتی را که نوشتن کتابی بالینی بر دوش انسان می‌گذارد درک کنم؛ مسئولیت انتقال دقیق دانشی که بر مبنای تمامی شواهد موجود شکل گرفته است. این وظیفهٔ مهم با گسترش انفجارگونهٔ گزارش‌های پزشکی و علمی در هر دهه خطیر تر نیز شده است. و با این حال، حتی امروز نیز پدیده‌ای فیزیولوژیکی و اختلال‌های پاتولوژیکی وجود دارند که به‌طور کامل موفق به درک آنها نشده‌ایم. به همین دلیل، نویسندگانی که کتابی بالینی می‌نویسند باید همچنان به تجربهٔ خود اتکا کنند و بر آن مبنا درک خود از

بیماری‌ها و مراقبت از بیماران را قضاوت نمایند.
امیدوارم این کتاب که هدفش درمان بیماران است همچنان مورد استفادهٔ دانشجویان، رزیدنت‌ها و پزشکان قرارگیرد. من به خوبی می‌دانم که نگارش کتاب‌های پزشکی بالینی نیاز به چه تلاش گسترده‌ای دارد. و به همین خاطر، از صمیم قلب از همکاران در دانشگاه یِیل به خاطر تعهد و تلاش‌شان برای به ثمر رساندن ویرایش نهم این کتاب تشکر می‌کنم.

لئون اسپیروف، M.D
استاد زنان و زایمان و ژنیکولوژی
دانشگاه علم و سلامت اورگون
پورتلند، اورگون

مقدمه

نگارش اندوکرینولوژی ژنیکولوژیک اسپیروف برای ما افتخار بسیار بزرگی است. این کتاب جزو یکی از کتاب‌های اصلی در این حوزهٔ پزشکی است. بسیاری از متخصصان این حوزه فیزیولوژی تولید مثل و اندوکرینولوژی را بر مبنای این کتاب آموخته‌اند. چطور می‌توان کتابی را که به یکی از آثار کلاسیک در حوزهٔ خاصی تبدیل شده است بازنویسی کرد؟ ما جسارت این را به خود ندادیم که در صدد اصلاح کتاب دکتر اسپیروف بر آییم، بلکه تلاش کردیم با افزودن اطلاعات جدید به این کتاب کلاسیک، آن را به روز کنیم. تمرکز خود را بر تغییرات و پیشرفت‌هایی که پس از چاپ ویرایش قبلی در این حوزه رخ داده است گذاشتیم. این مطالب تازه در فصل‌های مربوط به پزشکی تراجنسیتی و حفظ باروری آمده است. تا جایی که ممکن بود سبک و نثر دکتر اسپیروف را حفظ کردیم. به دکتر اسپیروف، به خاطر اعتمادی که به ما داشت، مدیون هستیم.

متن این کتاب در دپارتمان پزشکی زنان و زایمان و ژنیکولوژی در دانشکدهٔ پزشکی یِیل تدوین یافت. دکتر اسپیروف، گلس و کیز در زمان خود از اعضای هیئت علمی این دپارتمان بودند و در نگارش کتاب همکاری داشتند. با این حال، عشق دکتر اسپیروف به نوشتن و آموختن دانسته‌ها به دیگران باعث شد که در طول چاپ ویرایش‌های مختلف کتاب با آن همراه باشد و به‌طور مدام برای بهبود و گسترش آن تلاش کند. این کتاب همراه او به مؤسسه‌های دانشگاهی مختلفی سفر کرد. امروز، اندوکرینولوژی زنان و ناباروری اسپیروف بار دیگر به یِیل، یعنی محل تولدش، بازگشته است و این بار نویسندگان تازه‌ای از این دانشگاه آن را آمادهٔ چاپ کرده‌اند. بحث پیرامون انتقال این کتاب به یِیل در نشست انجمن پزشکی زنان و زایمان یِیل در نیو هِیوِن آغاز شد. در آن نشست، جایزهٔ ارزشمند دانش‌آموختگان دانشکده به دکتر اسپیروف اهدا شد. هنگامی که او پیشنهاد داد که کتاب را به خانهٔ قدیمی خودش بازگرداند، ما مشتاقانه استقبال کردیم.

این کتاب حاصل تلاش گروهی از نویسندگان و بسیاری از دست‌اندرکاران دیگر است. نویسندگان تمایل دارند علاوه بر دکتر اسپیروف، از دکتر مارک فریتز تشکر کنند که متن کتاب را در ویرایش‌های مختلف همراهی کرد. همکاری‌های او باعث شدند که اطلاعات کتاب طی سالیان مختلف به‌روز بماند. همچنین، از مؤسسهٔ انتشاراتی والترز کلوور به خاطر پشتکار، تلاش و تشویق‌هایش در طول مسیر سپاسگزاریم.

به ویژه، از کریس تیا و اَشلی فیشر متشکریم که با مهارت‌های مدیریتی خودشان کمک کردند که کتاب به‌موقع به چاپ برسد.
امیدواریم که خوانندگان این کتاب از این کتاب نهایت بهره را ببرند، درست همان‌طور که ما در طول تحصیل و کار خود از آن استفاده کرده‌ایم. هیچ چیز برای ما ارزشمندتر از آن نیست که بتوانیم نسل بعدی متخصصان زنان و زایمان را آموزش دهیم.

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لوبنا پَل، MBBS, MS
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مقدمه ترجمه فارسی

سپاس فراوان خداوند منان را که سعادت را همراهمان نمود تا بتوانیم خدمتی را در راه تعالی دانش پزشکی در زمینهٔ اندوکرینولوژی بالینی زنان و ناباروری تقدیم جامعه نماییم. کتابی که در دست شماست ویرایش نهم کتاب اندوکرینولوژی بالینی زنان و ناباروری اسپیروف است که حاصل اندیشه‌های گرانقدر و تجربیات آموزشی و فعالیت‌های بالینی افرادی است که سالیان متمادی عمر خود را صرف آموزش و پژوهش نموده‌اند. در طول چند دههٔ اخیر پیشرفت‌های حاصل در زمینهٔ اندوکرینولوژی و ناباروری بسیار چشمگیر بوده، به طوری که با تغییر نگرش‌ها در مکانیسم عملکرد هورمون‌ها و همچنین با استفاده از روش‌های کمک‌باروری روند کلی پیگیری و درمان ناباروری را متحول ساخته است.

همکاران جوان ما به حمدالله از نعمت تسلط به زبان انگلیسی و درک و انتقال مفاهیم برخوردار بوده و ذوق خویش را به ارائه کتابی استاندارد معطوف نموده‌اند، به طوری که ترجمهٔ ویرایش نهم کتاب اندوکرینولوژی بالینی زنان و ناباروری اسپیروف را عهده‌دار شده‌اند که راهنمای بین‌المللی همکاران در سرتاسر جهان می‌باشد.

خوشبختانه مترجمان این کتاب ارزشمند، دکتر مهرناز ولدان که خود متخصص این رشته هستند به اتفاق همکاران‌شان دکتر مینا فتحی، دکتر سیامک ملکی، دکتر مهشید نیکپور و دکتر سهراب نوذری، با توجه به شناخت عمیق از مفاهیم کتاب، ترجمه‌ای را هدیه نموده‌اند که از هر لحاظ شایان تقدیر است. کتاب به گونه‌ای طراحی شده است که متخصصان زنان و علاقه‌مندان بتوانند در زمانی کوتاه از اطلاعات کامل در زمینهٔ اندوکرینولوژی بالینی و ناباروری بهره‌مند گردند. بنده توفیق انجام این کار فاخر را به همکاران گرامی که با دقت نظر توانسته‌اند به سرعت این اثر را در اختیار همکارانشان قرار دهند تبریک عرض می‌کنم و از درگاه ایزد منان آرزوی تندرستی و موفقیت در ادامهٔ فعالیتشان دارم. مطالعهٔ این کتاب را برای به روز شدن دانش ناباروری به تمامی متخصصان این حوزه توصیه می‌کنم.

همچنین، از انتشارات محترم کتاب ارجمند که در پیشبرد اهداف عالیهٔ دانش پزشکی در چند سال اخیر از هیچ گونه حمایت و تلاشی دریغ ننموده‌اند سپاسگزارم.

دکتر فیروزه اکبری اسبق

استاد دانشگاه علوم پزشکی تهران

جراح و متخصص زنان و زایمان ـ فلوشیپ نازایی و IVF

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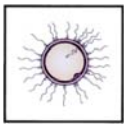

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تولید زیستی، متابولیسم و مکانیسم عمل هورمون‌ها

تعریف کلاسیک هورمون بدین شرح است: ماده‌ای که در یک بافت خاص تولید شده، از آن جا وارد گردش خون گشته، توسط خون به سلول‌های پاسخ‌دهنده دوردست رسیده و در این سلول‌ها اثرات خاصی را اعمال می‌نماید. آنچه که زمانی به عنوان سفری ساده در نظر گرفته می‌شد، امروزه با عنایت به پژوهش‌های صورت گرفته در آزمایشگاه‌های سراسر جهان و آشکارشدن جنبه‌های جدیدی از این مسیر، به عنوان یک سفر پرحادثهٔ پیچیده در نظر گرفته می‌شود. در حقیقت این عقیده که هورمون‌ها تنها در بافت‌های خاصی تولید می‌شوند، به چالش کشیده شده است.

این نکته که هورمون‌های پیچیده و گیرنده‌های هورمونی در ارگانیسم‌های تک‌سلولی ابتدایی یافت شده‌اند، نشان می‌دهد که غدد درون‌ریز، پدیده‌ای قدیمی در فرآیند تکامل هستند. هورمون‌ها باید پش از انشعاب یافتن گیاهان و جانوران پدید آمده باشند زیرا مواد گیاهی بسیاری شبیه هورمون‌ها و گیرنده‌های هورمونی یافت می‌شود. ظرفیت وسیع سلول‌ها در تولید هورمون‌ها، توجیه‌کننده کشف هورمون‌ها در مکان‌هایی غریب می‌باشد (مثلاً تولید هورمون‌های گوارشی در مغز، وجود هورمون‌های جنسی در ترشحات روده). علاوه بر این، به دلیل آن که همه سلول‌ها ژن‌های لازم را برای بیان هورمون‌ها دارند، غافلگیرکننده نیست که سلول‌های سرطانی تمایز نیافته می‌تواند بیان ژن را آشکار کرده و در محل و زمان‌های نامناسب، هورمون تولید کنند.

هورمون‌ها یکی از ابزارهای ارتباطی بوده و اکنون باید به‌طور گسترده‌تر به عنوان مواد شیمیایی تنظیم‌کننده و پیام‌رسان شناخته شوند. هورمون‌های درون‌ریز به‌طور کلاسیک در جریان خون به مناطق دوررس می‌روند امّا ارتباطات سلولی نیز در موضع مورد نظر مهم هستند. تعاملات پاراکرین، اتوکرین و اینتراکرین، اشکالی بی‌واسطه‌تر از ارتباط می‌باشند. در مقام مقایسه با پیام‌های درون‌ریز که در محل‌های دور اثر می‌کنند، پاراکرین به عنوان ارتباطی بین سلولی که مستلزم انتشار موضعی مواد تنظیم‌کننده از یک سلول به سلول مجاور می‌باشد، تعریف می‌شود. در مورد بعدی، ارتباط اتوکرین و اینتراکرین به عنوان ارتباطی داخل سلولی تعریف می‌شوند که مواد تنظیم‌کننده‌ای ترشح می‌کند که بر روی گیرنده‌های همان سلول عمل می‌کنند و در مورد اینتراکرین مواد ترشح نشده به گیرنده‌های داخل سلولی متصل می‌شوند.

حال بیایید گردش یک مولکول استرادیول را پیگیری نموده و بدین وسیله دیدی کلی را در مورد نحوه تولید، عملکرد و متابولیسم هورمون‌ها به دست آوریم. عمر استرادیول با ساخت آن در سلول‌هایی که اختصاصاً بدین منظور سازگاری یافته‌اند، آغاز می‌گردد. برای انجام تولید زیستی، لازم است علاوه بر وجود پیش‌سازهای مناسب، فعالیت آنزیم نیز به صورت صحیح باشد. در زنان بالغ، منابع اصلی استرادیول سلول‌های گرانولوزای فولیکول‌های در حال رشد و جسم زرد می‌باشند. این سلول‌ها قابلیت آن را دارند که در پاسخ به محرک‌های اختصاصی، استروئید تولید نمایند. عوامل محرک عبارتند از: گنادوتروپین‌ها، هورمون تحریک‌کننده فولیکول (FSH) و هورمون زردینه‌ساز (LH). مرحله ابتدایی این فرآیند که به تولید استرادیول منجر می‌شود، شامل انتقال پیام از عوامل محرک به مکانیسم‌های تولید استروئید در داخل سلول‌ها می‌باشد.

پیام‌های محرک استروئیدوژنز بایستی از خلال غشای

سلولی انتقال یابند. این انتقال ضروری است، زیرا گنادوتروپین‌ها، گلیکوپپتیدهای بزرگی هستند که به‌طور طبیعی نمی‌توانند وارد سلول شوند، اما بایستی با اتصال به گیرنده‌های موجود بر روی سلول‌ها، با سلول ارتباط برقرار نمایند. به دنبال این امر، یک سلسله از ارتباطات فعال می‌گردد. بخش قابل‌توجهی از پژوهش‌ها معطوف به تعیین روش‌هایی است که توسط آنها، این ارتباطات صورت می‌پذیرد. در سال ۱۹۷۱، پژوهشگری به نام ساترلند، جایزه نوبل را به علت طرح مفهوم "پیامبر ثانویه" به خود اختصاص داد.

گنادوتروپین (پیامبر اولیه)، آنزیمی را در غشای سلول فعال می‌کند که آدنیلات سیکلاز نام دارد. این آنزیم با تسهیل تولید پیامبر ثانویه در داخل سلول، پیام هورمون را منتقل می‌کند. در این جا پیامبر ثانویه، آدنوزین ′۳،′۵– منوفسفات حلقوی (AMP حلقوی) می‌باشد. پیام از گنادوتروپین به AMP حلقوی منتقل می‌گردد (مانند تبادل چوب در مسابقهٔ دو امدادی).

AMP حلقوی (پیامبر ثانویه) آغازگر فرایند استروئیدوژنز است؛ این فرایند به تولید و ترشح هورمون استرادیول ختم می‌شود. با درک برخی مفاهیم فیزیولوژیک (مانند ناهمگونی هورمون‌های پپتیدی، تنظیم افزایشی و کاهشی[1] گیرنده‌های غشای سلول، تنظیم فعالیت آدنیلات سیکلاز، و نقش مهم فاکتورهای تنظیم‌کننده اتوکرین و پاراکرین) تصویر ساختن مفهوم انتقال پیام، بسیار پیچیده‌تر شده است.

ترشح استرادیول به درون گردش خون، مستقیماً به دنبال ساخت آن روی می‌دهد. استرادیول در گردش خون به دو شکل حضور دارد: فرم آزاد و فرم اتصال یافته. بخش اعظم هورمون به پروتئین‌های ناقل (آلبومین و گلوبولین متصل‌شونده به هورمون‌های استروئیدی جنسی) اتصال دارد. به دنبال این اتصال، فعالیت زیستی هورمون محدود شده و بدین وسیله از بروز واکنش‌های بیش از حد یا ناگهانی جلوگیری می‌شود. به علاوه، این اتصال از متابولیسم سریع و بی‌مورد هورمون ممانعت نموده و بدین وسیله این امکان فراهم می‌شود که به منظور اطمینان از اِعمال اثر زیستی، هورمون به مدت لازم وجود داشته باشد. این مکانیسم شبه ذخیره‌ای، از فراز و نشیب‌های سطح هورمون جلوگیری کرده و امکان ایجاد سطح ثابت‌تری از عملکرد هورمون را فراهم می‌آورد.

اثرات زیستی و متابولیک هورمون توسط قابلیت سلول در پذیرش و حفظ آن تعیین می‌گردد. استرادیولی که به پروتئین متصل نباشد و آزادانه در خون گردش کند، به راحتی از طریق انتشار سریع وارد سلول می‌شود. با این حال برای آن که استرادیول اثرات خود را اعمال کند، باید در داخل سلول به یک گیرنده متصل گردد. نقش گیرنده، کمک به انتقال پیام هورمون است؛ پیام هورمون نهایتاً به رونویسی از ژن‌های هسته ختم می‌شود. نتیجه انتقال پیام، تولید RNA پیامبر است که به ساخت پروتئین و بروز پاسخ خاص سلول به هورمون منجر می‌شود.

پس از آن که استرادیول مأموریت خود را انجام داد، در نهایت مجدداً به گردش خون وارد می‌شود. این امکان وجود دارد که استرادیول پیش از متابولیزه شده و پاک شدن از گردش خون، وظیفه خود را چندین بار انجام دهد. از سوی دیگر، بسیاری از مولکول‌ها شانس آن را پیدا نمی‌کنند که اثر خود را حتی یک بار اعمال نمایند. برخلاف استرادیول، برخی هورمون‌ها (مانند تستوسترون) ممکن است در داخل سلول هدف، مستقیماً عمل نموده یا متابولیزه شده و تغییر یابند. در مورد اخیر، متابولیت تولید شده به عنوان ترکیبی غیرفعال، وارد گردش خون می‌گردد. پاک شدن استروئیدها از گردش خون، برحسب ساختار مولکولی آنها متفاوت است.

سلول‌هایی که قادر به پاکسازی استرادیول از گردش خون می‌باشند، این عمل را از طریق ابزارهای شیمیایی (تبدیل به استرون یا استریول که به ترتیب دارای اثربخشی متوسط و بسیار ضعیف می‌باشند) و کنژوگه کردن استرادیول و تبدیل آن به ماده‌ای محلول در آب که قابل دفع از طریق ادرار و صفرا می‌باشد (کنژوگه‌های سولفو[2] و گلوکورو[3]) انجام می‌دهند.

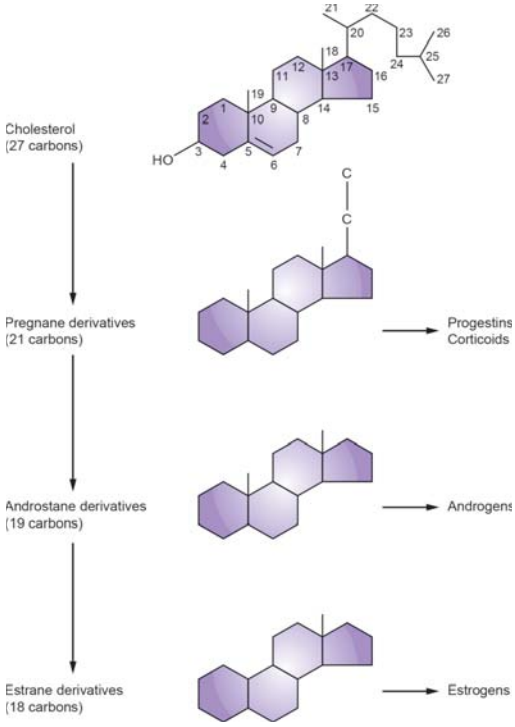
بنابراین هورمون‌های استروئیدی در طول عمر کوتاه خود وظایف متنوعی برعهده دارند. در این فصل، بخش‌های مهم عمر یک هورمون استروئیدی به‌طور مفصل‌تر و همچنین فرآیندهایی که طی آن هورمون آزادکننده ترشح هورمون‌های استروئیدی را تنظیم می‌کنند مورد بحث قرار خواهد گرفت.

ساختار هورمون‌های استروئیدی

تمام هورمون‌های استروئیدی دارای ساختار پایه‌ای مشابهی هستند و تفاوت‌های شیمیایی نسبتاً جزئی آنها منجر به تغییرات

1- up-and down-regulation

2- sulfo 3- glucuro



شکل ۱-۱

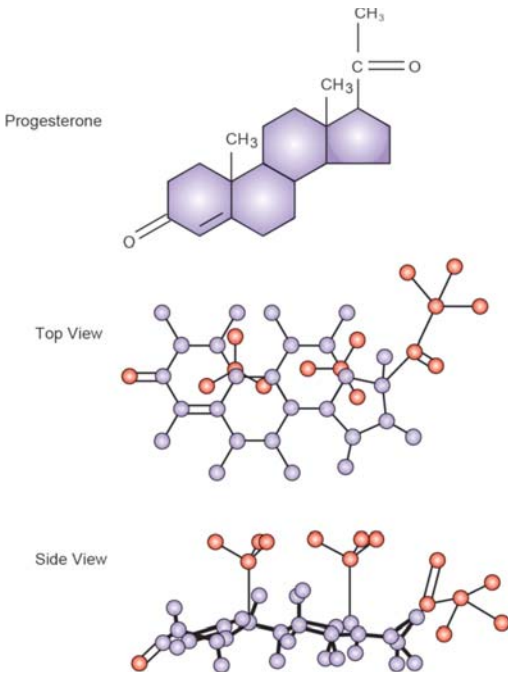
قابل‌توجهی در فعالیت بیوشیمیایی آنها می‌گردد. ساختار پایه‌ای این هورمون‌ها، شامل مولکول پرهیدروسیکلوپنتان فنانترن[1] می‌باشد. این مولکول از سه حلقه ۶ کربنه و یک حلقه ۵ کربنه تشکیل شده است. این ساختار شامل یک حلقه ۶ کربنه بنزن، دو حلقه ۶ کربنه نفتالن و سه حلقه ۶ کربنه فنانترن می‌باشد؛ با اضافه شدن یک سیکلوپنتان (حلقه ۵ کربنه)، ساختار پرهیدروسیکلوپنتان فنانترن هستهٔ استروئید حاصل می‌شود.

استروئیدهای جنسی براساس تعداد اتم‌های کربن به سه گروه اصلی تقسیم می‌شوند. استروئیدهای ۲۱ کربنه شامل کورتیکوئیدها و پروژستین‌ها بوده و ساختار پایه‌ای آنها شامل هسته **پرگنان**[2] است. استروئیدهای ۱۹ کربنه شامل تمام آندروژن‌ها بوده و شالوده آنها هسته **آندروستان**[3] است، حال آن که استروئیدهای ۱۸ کربنه دارای هسته **استران**[4] هستند **(شکل ۱-۱)**.

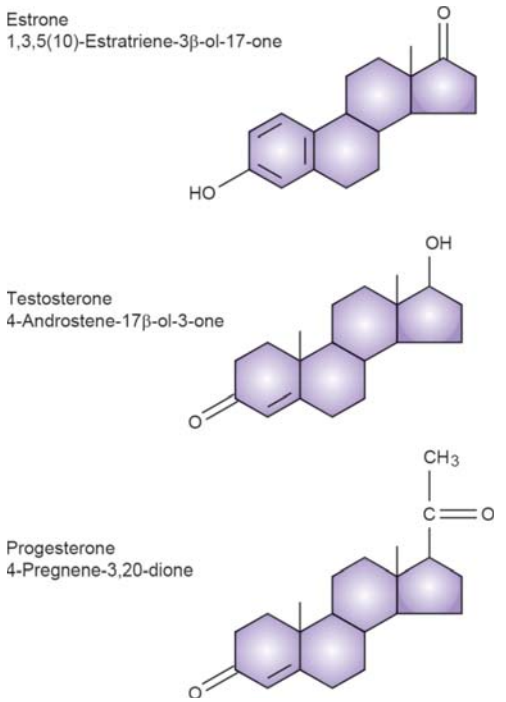
برروی ساختار حلقوی پایه‌ای، ۶ مرکز عدم‌تقارن وجود داشته و از این رو ۶۴ ایزومر ممکن است وجود داشته باشد. تقریباً تمام استروئیدهای فعالی که به‌طور طبیعی وجود دارند، دارای ساختاری مسطح بوده و استخلاف‌های موجود در بالا و پایین این صفحه، به ترتیب با آلفا (α) (خط نقطه‌چین) و بتا (β) (خط ممتد) نشان داده می‌شوند. تغییر موقعیت تنها یک استخلاف می‌تواند منجر به تولید ایزومرهای غیرفعال شود. به عنوان مثال، ۱۷- اپی‌تستوسترون به نحو قابل‌توجهی ضعیف‌تر از تستوسترون است؛ تنها تفاوت این دو در این است که به جای آن که گروه هیدروکسیل در C-17 در موقعیت β قرار داشته باشد، در موقعیت α قرار گرفته است **(شکل ۲-۱)**.

برای اشاره به ساختار پایه‌ای (مانند پرگنان، آندروستان و استران)، طبق قرارداد، در نامگذاری استروئیدها از شمار اتم‌های کربن استفاده می‌شود. اعدادی که پیش از نام ساختار پایه‌ای قرار می‌گیرند، نشان‌دهنده موقعیت پیوندهای دوگانه است؛ برای اشاره به تعداد پیوندهای دوگانه، نام این ساختار به شرح زیر تغییر می‌کند: -اِن[5] (یک پیوند دوگانه)، -دی‌اِن[6] (دو پیوند دوگانه) و -تری‌ان[7] (سه پیوند دوگانه). پس از نام ساختار پایه، گروه‌های هیدروکسیل براساس شماره کربنی که به آن اتصال دارند، نشان داده می‌شوند. برای اشاره به تعداد گروه‌های هیدروکسیل از قرارداد زیر استفاده می‌شود که به ترتیب برای یک، دو، یا **(شکل ۳-۱)** سه گروه هیدروکسیل می‌باشد: -اول[8]، -دیول[9]، و -تریول[10]. گروه‌های کتون با ذکر شماره کربنی که به آن اتصال دارند، در آخر عنوان می‌شوند؛ به وجود یک، دو، یا سه گروه کتون، به ترتیب از پسوندهای -اون[11]، -دیون[12] یا -تریون[13] استفاده می‌شود. اصطلاحات دیگر عبارتند از: دزوکسی (حذف اکسیژن)؛ نور[14] (حذف کربن) و دلتا (Δ) (موقعیت پیوند دوگانه).

1- perhydro cyclopentanephenanthrene
2- pregnane
3- androstane
4- estrane
5- ene
6- diene
7- triene
8- ol
9- diol
10- triol
11- one
12- dione
13- trione
14- nor



شکل ۲-۱



شکل ۳-۱

استروئیدوژنز

تولید هر سه گروه اصل استروئیدهای جنسی از یک مسیر بوده که با مولکول کلسترول آغاز می‌گردد. در این بخش، ما در مورد این تولید زیستی از تولید و دریافت کلسترول در طی ساخت هر کدام از استروئیدهای جنسی بحث خواهیم کرد.

لیپوپروتئین‌ها و کلسترول

کلسترول واحد ساختاری پایه‌ای در فرآیند استروئیدوژنز می‌باشد. تمام اندام‌های سازنده استروئید، به جز جفت می‌توانند کلسترول را از استات تولید نمایند. به این ترتیب بخش‌های مختلف بافت تخمدان می‌توانند به صورت درجا[1]، پروژستین‌ها، آندروژن‌ها و استروژن‌ها را از مولکول دو کربنه استات، از طریق کلسترول (پیش‌ساز مشترک استروئیدها) تولید نمایند. با این‌حال تولید درجا، نمی‌تواند پاسخگوی نیازها باشد؛ ازاین‌رو، خون منبع اصلی کلسترول به شمار می‌رود. کلسترول خون پس از ورود به سلول‌های تخمدان، وارد مسیر تولید زیستی شده یا جهت استفاده‌های بعدی به‌شکل استریفیه ذخیره می‌گردد. ورود کلسترول به درون سلول با واسطه گیرنده LDL برروی غشای سلول صورت می‌گیرد؛ LDL، ناقل کلسترول در گردش‌خون می‌باشد.

لیپوپروتئین‌ها مولکول‌های بزرگی هستند که انتقال چربی‌های غیرقطبی را در یک حلال قطبی (پلاسمای خون) تسهیل می‌کنند. لیپوپروتئین‌ها براساس بار و چگالی (حرکت در طی اولتراسانتریفیوژ) به پنج دسته اصلی تقسیم می‌شوند. این گروه‌ها طی آبشاری از واکنش‌های کاهش اندازه و افزایش چگالی، به یکدیگر تبدیل می‌شوند.

1- in situ

شیلومیکرون‌ها

ذرات بزرگ حمل‌کننده کلسترول (۱۰٪) و تری‌گلیسرید (۹۰٪) که پس از صرف غذای چرب در روده تشکیل می‌شوند.

لیپوپروتئین با چگالی بسیار پایین (VLDL)

عمدتاً ناقل تری‌گلیسرید می‌باشد؛ اما کلسترول را نیز حمل می‌کند. VLDL چگال‌تر از شیلومیکرون‌ها می‌باشد.

لیپوپروتئین با چگالی متوسط (IDL)

با برداشت مقداری از تری‌گلیسرید از بخش داخلی ذرات VLDL، تشکیل می‌گردد (به عنوان یک ذره موقت).

لیپوپروتئین با چگالی پایین (LDL)

محصول نهایی کاتابولیسم VLDL بوده و به دنبال برداشت بیشتر تری‌گلیسرید حاصل می‌شود؛ نهایتاً LDL حاوی ۵۰٪ کلسترول خواهد بود؛ LDL ناقل اصلی (دوسوم) کلسترول در پلاسما بوده و از این رو ارتباطی قوی بین سطح بالای LDL و بیماری‌های قلبی ـ عروقی وجود دارد.

لیپوپروتئین با چگالی بالا (HDL)

کوچکترین و چگال‌ترین لیپوپروتئین با بیشترین محتوای پروتئین و فسفولیپید می‌باشد. سطح HDL با آترواسکلروز رابطه عکس دارد (سطوح بالای HDL نقش محافظتی دارد). HDL را می‌توان به یک بخش سبک‌تر (HDL_2) و یک بخش چگال‌تر (HDL_3) تفکیک نمود.

لیپوپروتئین‌ها دارای چهار ماده تشکیل‌دهنده هستند: (۱) کلسترول، که به دو شکل وجود دارد: کلسترول آزاد موجود بر سطح مولکول کروی لیپوپروتئین، و کلسترول استریفیه در بخش داخلی مولکول؛ (۲) تری‌گلیسرید در بخش داخلی مولکول؛ (۳) فسفولیپید؛ و (۴) مولکول‌های پروتئین که در ترکیبات باردار موجود بر سطح کره حضور داشته و مسئول تشکیل میسل با آب و پلاسما هستند. پروتئین‌های سطحی که **آپوپروتئین**[1] خوانده می‌شوند، جایگاه‌هایی را تشکیل می‌دهند که به مولکول‌های گیرنده لیپوپروتئین‌ها در سطح سلول‌ها متصل می‌شوند. پروتئین سطحی اصلی LDL، آپوپروتئین B بوده و آپوپروتئین A-1، آپوپروتئین اصلی HDL می‌باشد.

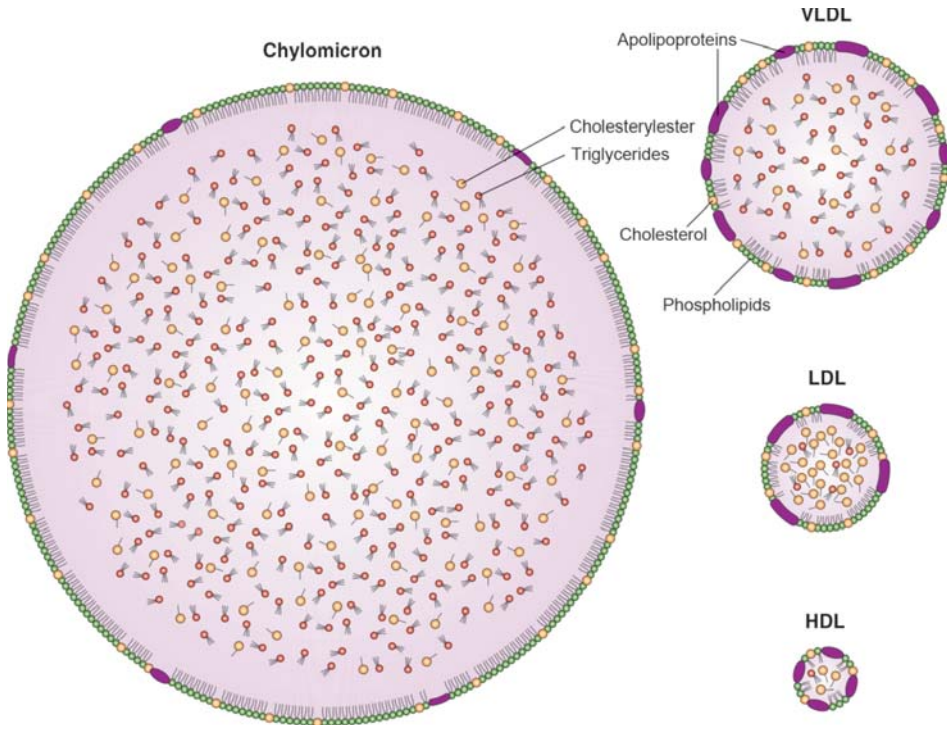
کبد با ترشح VLDL، لیپیدها را برای بافت‌های محیطی فراهم می‌سازد. تری‌گلیسریدها توسط لیپوپروتئین لیپاز موجود در سلول‌های اندوتلیال مویرگ‌ها و همچنین آنزیم لیپاز موجود در سلول‌های اندوتلیال سینوزوئیدهای کبدی، از VLDL آزاد می‌گردند. به دنبال این فرایند، اجزای سطحی (کلسترول آزاد، فسفولیپیدها و آپوپروتئین‌ها) به HDL منتقل می‌شوند. نهایتاً VLDL به LDL تبدیل می‌شود. LDL نقش مهمی را در انتقال کلسترول به سلول‌های سراسر بدن ایفا می‌کند. آنزیم لیپاز کبدی نسبت به تغییرات استروئیدهای جنسی حساس می‌باشد: این آنزیم توسط استروژن سرکوب و توسط آندروژن‌ها تحریک می‌گردد (شکل ۴-۱).

LDL توسط یک سری گیرنده‌های سلولی که یکی از آپوپروتئین‌های سطحی را شناسایی می‌کنند، از خون برداشته می‌شود. لیپوپروتئین متصل به گیرنده غشای سلولی، وارد سلول شده و تجزیه می‌گردد. بخشی از تنظیم سطح داخل سلولی کلسترول توسط تنظیم کاهش و افزایشی گیرنده‌های LDL موجود بر روی غشای سلولی صورت می‌گیرد. زمانی که گیرنده‌های LDL اشباع شده یا تعداد آنها کم باشد، LDL توسط سلول‌های "رفتگر"[2] (که عمدتاً از ماکروفاژها مشتق می‌گردند) در سایر بافت‌ها (خصوصاً لایه اینتیمای شریان‌ها) برداشت می‌شود. به این ترتیب، سلول‌های مزبور می‌توانند به عنوان هسته اولیه تشکیل پلاک‌های آترواسکلروز عمل کنند.

HDL توسط کبد و روده ترشح شده یا به دنبال تجزیه VLDL حاصل می‌شود. مولکول‌های استر کلسترول، هسته‌ای را در یک ذره کروی کوچک (ذره HDL_3) تشکیل می‌دهند. این ذرات، کلسترول آزاد اضافه را (احتمالاً با واسطه گیرنده‌هایی که آپوپروتئین A-1 را شناسایی می‌کنند) جذب می‌کنند. به دنبال برداشت کلسترول، اندازه ذره افزایش یافته و بدین ترتیب ذره HDL_2 تشکیل می‌گردد؛ HDL_2، بخشی است که منعکس‌کننده تغییرات رژیم غذایی و هورمون‌هاست. سطح HDL_3 نسبتاً پایدار می‌ماند.

بخش پروتئینی ذرات لیپوپروتئین قویاً با خطر بیماری‌های قلبی ـ عروقی در ارتباط است؛ بروز ناهنجاری‌های ژنتیکی در ساخت یا ساختار این بخش می‌تواند منجر به حالات آتروژنیک شود. لیپوپروتئین‌ها یکی از علل اصلی نابرابری خطر آترواسکلروز بین زنان و مردان هستند. در دوران بزرگسالی، سطح HDL ـ کلسترول خون حدود ۱۰mg/dL در زنان بالاتر است؛ این تفاوت در دوران پس از یائسگی نیز ادامه دارد. سطح

1- apoprotein
2- scavenger cells



شکل ۴-۱

تام کلسترول و سطح LDL ـ کلسترول در زنان، پیش از یائسگی از مردان پایین‌تر است، اما پس از یائسگی این سطوح به سرعت افزایش می‌یابد.

ماهیت محافظت‌کنندگی HDL، ناشی از قابلیت آن در برداشت کلسترول آزاد از سلول‌ها یا لیپوپروتئین‌های در گردش است. این HDL غنی از لیپید، که تحت عنوان HDL_3 خوانده می‌شود، در مراحل بعد به ذرات HDL_2 تبدیل می‌شود که اندازه بزرگ‌تر و چگالی کمتری دارد. به این ترتیب، HDL سلول‌های رفتگر غنی از لیپید (ماکروفاژهای مقیم دیواره‌های شرائین) را به حالت کم لیپید قبلی برگردانده و کلسترول اضافی را به مکان‌هایی انتقال می‌دهند (عمدتاً کبد) که قابلیت متابولیزه کردن کلسترول را داشته باشند. روش دیگری که طی آن HDL کلسترول را از بدن برداشت می‌نماید، مبتنی بر برداشت کلسترول آزاد از غشاهای سلولی است. کلسترول آزاد، استریفیه شده و به هسته ذرات HDL منتقل می‌گردد. به این ترتیب، HDL می‌تواند با تحویل کلسترول به جایگاه‌های مختلف، جهت استفاده (سلول‌های تولیدکننده استروئید) یا متابولیسم و دفع (کبد)، کلسترول را برداشت نماید.

به منظور نیل به سلامت قلبی ـ عروقی، غلظت خونی کلسترول باید پایین نگه داشته شده و از گریز آن از گردش خون جلوگیری شود. مشکل نقل و انتقال کلسترول از طریق استریفیه شدن کلسترول و بسته‌بندی استر در داخل هسته‌های لیپوپروتئین‌های پلاسما برطرف شده است. انتقال کلسترول به درون سلول‌ها نیز به نوبه خود توسط گیرنده‌های لیپوپروتئین حل گردیده است. پس از اتصال لیپوپروتئین با بسته کلسترول استریفیهٔ آن، کمپلکس حاصله از طریق اندوسیتوز وابسته به گیرنده، وارد سلول می‌گردد (این مطلب در ادامه مورد بحث قرار خواهد گرفت)؛ طی این فرایند، لیزوزوم‌ها کلسترول را جهت استفاده توسط سلول آزاد می‌نمایند.

حفاظت اصلی در برابر آترواسلکروز به میل بالای این

گیرنده‌ها به LDL و نیز قابلیت این گیرنده‌ها در بازیافت شدن به دفعات متعدد بستگی دارد؛ این امر امکان انتقال مقدار زیادی کلسترول را با حفظ سطح LDL در محدوده‌ای پایین و مناسب فراهم می‌کند. سلول‌ها می‌توانند برداشت کلسترول را براساس سطح داخل سلولی کلسترول و از طریق افزایش یا کاهش تعداد گیرنده‌های LDL کنترل نمایند. رژیم غنی از کلسترول با اثر بر روی کبد، باعث کاهش تعداد گیرنده‌های LDL در سطح سلول‌های کبدی شده و به این ترتیب، سطح LDL خون افزایش می‌یابد. استاتین‌ها از طریق کاهش تولید زیستی کلسترول، افزایش گیرنده‌های LDL در کبد و کاهش سطح LDL- کلسترول در گردش، فرد را در برابر آترواسلکروز محافظت می‌کنند.

مسیر بیوسنتز استروئید

مسیر کلی بیوسنتز استروئیدها که در **شکل ۵-۱** قابل رؤیت است، عمدتاً حاصل پژوهش‌های پیشگامانه کنت جی. رایان و همکاران وی است(۲،۱). این مسیرها از الگویی پایه‌ای تبعیت می‌کنند که در تمام اندام‌های درون‌ریز تولیدکننده استروئید مشاهده می‌شود. در نتیجه، چندان شگفت‌آور نیست که تخمدان‌ها در حالت طبیعی، هر سه گروه استروئیدهای جنسی را تولید می‌کنند: استروژن‌ها، پروژستین‌ها، و آندروژن‌ها. اهمیت آندروژن‌های تخمدان، نه تنها از آن حیث که پیش‌ساز اجباری استروژن‌ها به شمار می‌روند، بلکه به عنوان محصولات ترشحی مهم از نظر بالینی، قابل توجه است. تفاوت تخمدان با بیضه، در مجموعهٔ پایه‌ای آنزیم‌های حیاتی آن، و بنابراین تفاوت توزیع محصولات ترشحی آن می‌باشد. تفاوت تخمدان با غده فوق کلیه در این است که تخمدان فاقد ۲۱- هیدروکسیلاز و ۱۱β- هیدروکسیلاز می‌باشد. بنابراین، گلوکورتیکوئیدها و مینرالوکورتیکوئیدها در بافت طبیعی تخمدان تولید نمی‌شوند.

طی استروئیدوژنز، امکان کاهش تعداد اتم‌های کربن مولکول‌های کلسترول یا مولکول‌های استروئیدی دیگر وجود دارد، اما تعداد اتم‌های کربن هرگز افزایش نمی‌یابد. واکنش‌های زیر می‌توانند روی دهند:

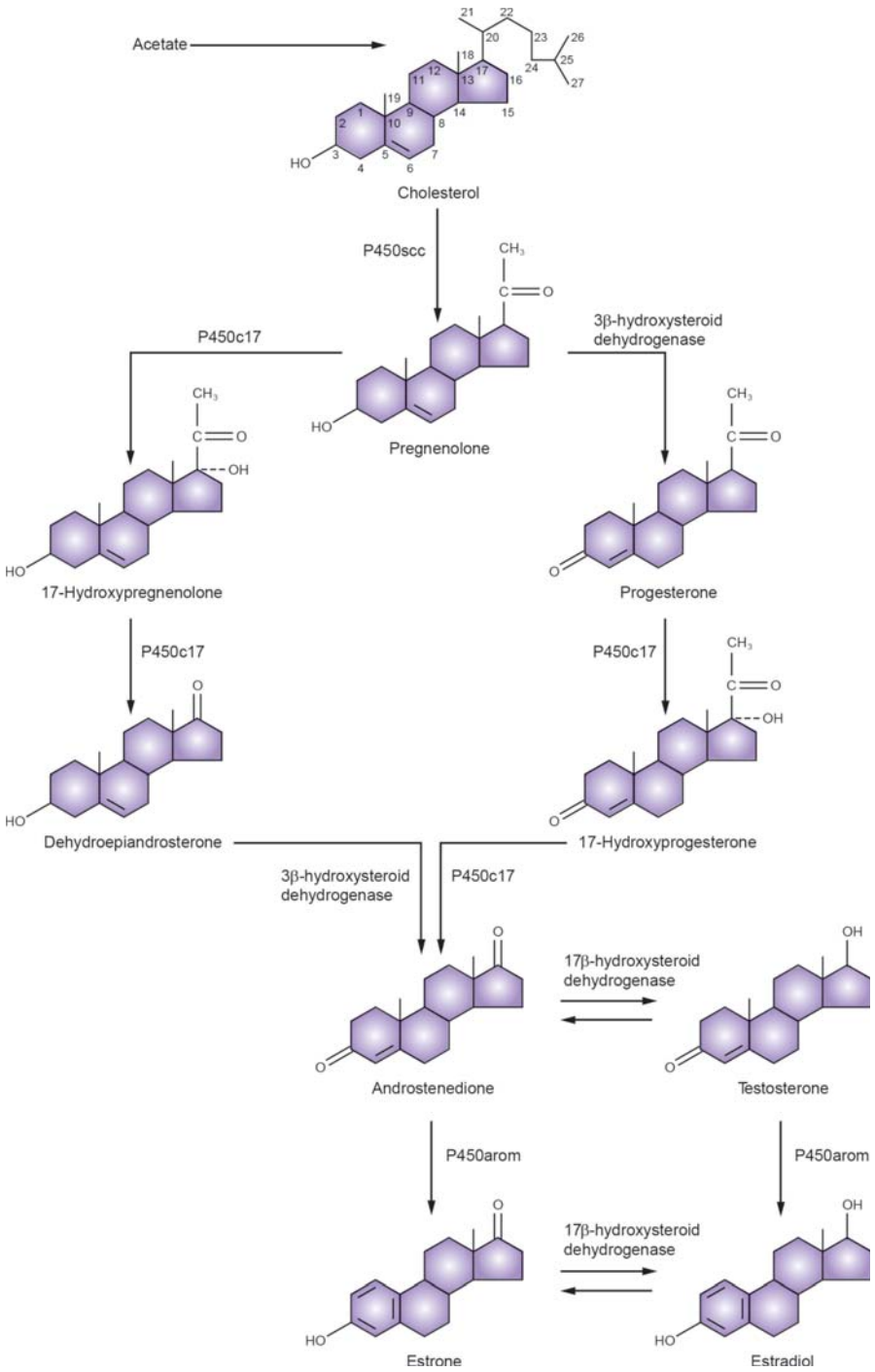
۱. **شکافت زنجیره جانبی (واکنش دسمولاز)**
۲. **تبدیل گروه‌های هیدروکسیل به گروه‌های کتون یا برعکس (واکنش‌های دهیدروژناز)**
۳. **افزودن گروه OH (واکنش هیدروکسیلاسیون)**
۴. **خلق پیوندهای دوگانه (برداشت هیدروژن)**
۵. **افزودن هیدروژن جهت احیای پیوندهای دوگانه (اشباع).**

دیدگاه سنتی در مورد استروئیدوژنز آن بود که هر مرحله توسط آنزیم‌های زیادی وساطت می‌گردد؛ این واکنش‌ها از بافتی به بافت دیگر متفاوت است. سادگی این سیستم زمانی هویدا شد که ژن‌ها و DNAهای مکمل مسئول این فرایند کلون شدند(۵-۳).

آنزیم‌های استروئیدساز، یا جزء دهیدروژناز بوده و یا از اکسیدازهای گروه سیتوکروم P450 هستند. سیتوکروم P450 یک اصطلاح کلی برای اشاره به خانواده‌ای از آنزیم‌های اکسیداتیو است؛ اصطلاح 450، به تغییر جذبی رنگدانه‌ای (450) در زمان احیا شدن اشاره دارد. آنزیم‌های P450 می‌توانند سوبستراهای زیادی را متابولیزه کنند؛ به عنوان مثال در کبد، آنزیم‌های P450، توکسین‌ها و آلوده‌کننده‌های محیطی را متابولیزه می‌نمایند. ژنوم انسان حاوی ژن‌های مربوط به ۵۷ آنزیم سیتوکروم P450 است (۷ آنزیم در میتوکندری و ۵۰ آنزیم در شبکه اندوپلاسمی؛ شبکه اندوپلاسمی، جایگاه اصلی پاکسازی متابولیک است). آنزیم‌های P450 زیر در استروئیدوژنز نقش دارند: P450scc، آنزیم شکافت زنجیره جانبی کلسترول است؛ P450c11 واسطهٔ ۱۱- هیدروکسیلاز، ۱۸- هیدروکسیلاز و ۱۹- متیل‌اکسیداز می‌باشد؛ P450c17 واسطه ۱۷- هیدروکسیلاز و ۱۷،۲۰- لیاز بوده و P450c21 واسطه ۲۱- هیدروکسیلاز می‌باشد؛ P450arom واسطه آروماتیزاسیون آندروژن‌ها به استروژن‌ها است **(جدول ۱-۱)**. تفاوت‌های جالب توجه در سازماندهی اگزون ـ اینترون ژن‌های p450، با منشأ باستانی این ژن‌ها سازگار است؛ به این ترتیب، ابرخانواده ژن‌های P450، بیش از ۱/۵ میلیارد سال پیش ظاهر شده‌اند.

با شناخت ساختار آنزیم‌های P450 که حاصل مطالعات تعیین توالی نوکلئوتیدها و اسیدهای آمینه است، مشخص شد که تمام مراحل مابین کلسترول و پرگننولون[1] با واسطهٔ یک پروتئین منفرد به نام P450scc صورت می‌گیرند. این پروتئین به غشای داخلی میتوکندری متصل است. داده‌های حاصل از مشابه سازی

1- pregnenolone


Acetate
Cholesterol
P450scc
Pregnenolone
P450c17
3β-hydroxysteroid dehydrogenase
17-Hydroxypregnenolone
Progesterone
P450c17
P450c17
Dehydroepiandrosterone
17-Hydroxyprogesterone
3β-hydroxysteroid dehydrogenase
P450c17
17β-hydroxysteroid dehydrogenase
Androstenedione
Testosterone
P450arom
P450arom
17β-hydroxysteroid dehydrogenase
Estrone
Estradiol

شکل ۵-۱

۱

جدول ۱-۱ آنزیم‌های سیتوکروم P450

آنزیم	موقعیت سلولی	واکنش‌ها
P450scc	میتوکندری	شکافت زنجیره جانبی کلسترول
P450c11	میتوکندری	۱۱-هیدروکسیلاز ۱۸-هیدروکسیلاز ۱۹- متیل اکسیداز
P450c17	شبکه اندوپلاسمی	۱۷-هیدروکسیلاز، ۱۷،۲۰- لیاز
P450c21	شبکه اندوپلاسمی	۲۱-هیدروکسیلاز
P450arom	شبکه اندوپلاسمی	آروماتاز

نشان داده‌اند که این پروتئین حامل رمزگردانی ژن *CYP11A1* بر روی کروموزوم ۱۵ می‌باشد. این تجربیات نشان می‌دهند که مراحل متعدد یک فرآیند به آنزیم‌های متعدد نیاز ندارند. تفاوت فعالیت در بافت‌های مختلف ممکن است منعکس‌کنندهٔ تغییرات پساترجمه‌ای باشد. به علاوه ژن‌های سازنده P450 حاوی توالی‌های پیش‌برنده[1] اختصاصی بافت هستند. این امر دلیل دیگری است که نشان می‌دهد مکانیسم‌های تنظیمی می‌توانند در بافت‌های مختلف (مانند جفت و تخمدان) متفاوت باشند. جهش‌های *CYP11A1*، بسیار نادر بوده و باعث مختل شدن استروئیدوژنز در غدد فوق کلیه و گنادها می‌شود؛ این اختلال موجب بروز تکامل جنسی غیرطبیعی و نارسایی فوق کلیه می‌گردد(۶).

تبدیل کلسترول به پرگننولون مستلزم هیدروکسیلاسیون در موقعیت کربن‌های ۲۰ و ۲۲ و متعاقباً جداشدن زنجیره جانبی می‌باشد. تبدیل کلسترول به پرگننولون (توسط P450scc) در داخل میتوکندری صورت می‌گیرد. این واکنش، یکی از اثرات اصلی تحریک هورمون‌های تروپیک است که موجب برداشت سوبسترای کلسترول جهت این مرحله در تخمدان نیز می‌گردد. هورمون‌های تروپیک هیپوفیز قدامی با اتصال به گیرنده سطح سلولی سیستم پروتئین G، آدنیلات سیکلاز را فعال نموده و باعث افزایش غلظت داخل‌سلولی AMP حلقوی می‌گردند. فعالیت AMP حلقوی منجر به رونویسی از ژن کدکننده آنزیم‌های استروئیدساز و پروتئین‌های فرعی می‌شود. طی فرآیندی که سریع‌تر از رونویسی ژن است، AMP حلقوی باعث تحریک هیدرولیز استرهای کلسترول و انتقال کلسترول آزاد به درون میتوکندری می‌گردد.

کلسترول مورد استفاده برای سنتز استروئیدها از LDL خون و در گام بعد آزادشدن و انتقال ذخایر داخل سلولی مشتق می‌شود(۸،۷،۵). هورمون‌های تروپیک با تحریک اندوسیتوز از طریق حفره‌های پوشیده از کلاترین (مکانیسمی که در ادامه مورد بحث قرار خواهد گرفت) موجب وارد شدن استرهای کلسترول LDL به درون سلول‌ها می‌شوند. در داخل سلول‌ها، کلسترول به شکل استر یا کلسترول آزاد ذخیره می‌گردد. در حقیقت، مرحله محدودکننده سرعت در فرآیند استروئیدوژنز، انتقال کلسترول از غشای خارجی میتوکندری به غشای داخلی میتوکندری می‌باشد؛ در غشای داخلی میتوکندری، P450scc کاملاً فعال در انتظار سوبسترا می‌باشد. انتقال محدودکننده سرعت کلسترول آب‌گریز از طریق فضای آبی بین غشاهای داخلی و خارجی میتوکندری با واسطه فعال شدن پروتئین‌ها در اثر تحریک هورمون‌های تروپیک صورت می‌گیرد. استروئیدسازی مزمن و طولانی‌مدت مستلزم رونویسی از ژن‌ها و ساخت پروتئین می‌باشد، اما پاسخ‌های حاد و کوتاه‌مدت، مستقل از سنتز RNA جدید است، با این حال ساخت پروتئین همچنان ضروری می‌باشد (به خصوص پروتئین‌های تنظیم‌کننده انتقال کلسترول از خلال غشای میتوکندری).

پروتئین‌های متعددی به عنوان تنظیم‌کننده انتقال حاد داخل سلولی کلسترول شناسایی و مطرح شده‌اند. SCP2[2] قادر است به کلسترول متصل شده و کلسترول را بین بخش‌های مختلف سلول جابه‌جا کند. پروتئین‌های نامزد دیگر عبارتند از: مولکول کوچک SAP[3] و PBR[4] (که مورد اخیر جریان کلسترول را از خلال ساختارهای منفذدار متأثر می‌سازد). اما شناخته‌شده‌ترین و مورد توجه‌ترین پروتئینی که به عنوان **تنظیم‌کننده انتقال حاد کلسترول مطرح است، پروتئین StAR[5] می‌باشد(۱۳-۹).** پروتئین‌ها و RNA پیامبر StAR، در پاسخ به تحریک AMP حلقوی، به‌طور همزمان با استروئیدوژنز حاد القا می‌گردند. پروتئین StAR باعث افزایش تولید استروئیدها می‌شود؛ این پروتئین وارد میتوکندری شده و در آنجا مستقر می‌گردد. هیپرپلازی لیپوئیدی مادرزادی فوق کلیه (نوعی اختلال اتوزومی مغلوب) حاصل مختل شدن استروئیدوژنز فوق کلیه و گنادها در اثر وقوع جهش‌های مختلف

1- promoter
2- sterol carrier protein 2
3- steroidogenesis activator polypeptide
4- peripheral benzodiazepine receptor
5- steroidogenic acute regulatory

در *StAR* است(۱۵،۱۴). به دنبال جهش‌های فراوان، امکان کاهش سطح استروئیدوژنز و حتی زنانه‌شدن[1] در هنگام بلوغ وجود دارد، اما ادامه تحریک هورمون‌های تروپیک باعث تجمع رسوبات لیپیدی در داخل سلول‌ها می‌شود که این امر، از بین رفتن قابلیت استروئیدوژنز را در پی دارد(۱۶). جهش‌های ژن StAR تنها بیماری ارثی استروئیدوژنز بوده که با اختلال در یکی از آنزیم‌های استروئیدوژنز همراه نیست.

StAR برای استروئیدوژنز فوق کلیه و گنادها لازم بوده (دلیل نقش واسطه‌گری در انتقال کلسترول به میتوکندری) و از این رو جهت تمایز نرمال جنسی یک فرد مذکر ضروری می‌باشد. StAR، کلسترول را از غشای خارجی میتوکندری به غشای داخلی میتوکندری منتقل می‌کند تا در آن جا از طریق تبدیل شدن به پرگننولون، وارد مسیر استروئیدوژنز شود. گروهی از پروتئین‌هایی که از لحاظ ساختاری مرتبط با StAR هستند شناسایی شده‌اند که به صورت StARD4، StARD5 و StARD6 نشان داده می‌شوند. StARD4، پس از تولید کلسترول آزاد در سیتوپلاسم، به آن متصل شده و آن را به غشای خارجی میتوکندری منتقل می‌کند(۱۲). از آن جایی که سلول‌های تولیدکننده استروئید، مقادیر زیادی از هورمون را ذخیره نمی‌کنند، افزایش حاد تولید هورمون‌ها، جهت ساخت سریع به این سیستم وابسته است.

پس از تولید پرگننولون، ادامه سنتز استروئیدها در تخمدان از طریق یکی از دو مسیر زیر صورت می‌گیرد: مسیر Δ^5-3β-هیدروکسی‌استروئید یا مسیر Δ^4-۳-کتون. مسیر نخست (مسیر Δ^5) از طریق پرگننولون و دهیدرواپی‌آندروسترون (DHEA) و مسیر دوم (مسیر Δ^4) از طریق پروژسترون و ۱۷α- هیدروکسی پروژسترون پیش می‌رود.

تبدیل پرگننولون به پروژسترون مستلزم طی دو مرحله است: واکنش‌های ۳β- هیدروکسی‌استروئید دهیدروژناز و $\Delta^{4\text{-}5}$ ایزومراز که باعث تبدیل گروه ۳- هیدروکسیل به نوعی کتون و نیز انتقال پیوند دوگانه از موقعیت ۶-۵ به موقعیت ۵-۴ می‌گردند. آنزیم ۳β- هیدروکسی‌استروئید دهیدروژناز که هر دو واکنش دهیدروژناسیون و ایزومریزاسیون را انجام می‌دهد به دو شکل (نوع I و نوع II) یافت می‌شود؛ این دو نوع، توسط دو ژن مجزا که بر روی کروموزوم ۱ قرار دارند رمزگردانی می‌گردند (نوع I در جفت، پستان و سایر بافت‌های غیرغده‌ای بیان می‌شود، اما نوع II در گنادها و غدد فوق‌کلیه بیان می‌گردد). به محض تشکیل $\Delta^{4\text{-}5}$ کتون، پروژسترون در موقعیت ۱۷- هیدروکسیله شده و بدین وسیله، ۱۷α- هیدروکسی‌پروژسترون حاصل می‌شود. در این مسیر، ۱۷α- هیدروکسی‌پروژسترون، پیش‌ساز حد واسط آندروژن‌های ۱۹ کربنی می‌باشد. با تشکیل پراکسید در موقعیت کربن ۲۰ و متعاقباً اپوکسیداسیون کربن‌های ۱۷ و ۲۰، زنجیره جانبی جدا شده و آندروستن‌دیون[2] حاصل می‌گردد. ۱۷-کتون ممکن است طی واکنش ۱۷β- هیدروکسی استروئید دهیدروژناز به یک ۱۷β- هیدروکسیل احیا شده و بدین طریق تستوسترون حاصل شود. این دو استروئید ۱۹ کربنه (آندروستن‌دیون و تستوسترون) می‌توانند طی یک سری واکنش‌های میکروزومی و طی فرآیندی که آروماتیزاسیون خوانده می‌شود، به استروژن‌های استروئید فنولیک ۱۸ کربنهٔ مربوطه (استرون و استرادیول) تبدیل شوند. این فرایند شامل هیدروکسیلاسیون گروه ۱۹- متیل‌آنگولار و متعاقباً اکسیداسیون و از دست رفتن کربن ۱۹ به شکل فرمالدهید و آروماتیزاسیون حلقه A (دهیدروژناسیون) می‌باشد. به عنوان جایگزین، پرگننولون می‌تواند طی ۱۷α- هیدروکسیلاسیون و متعاقباً جداشدن زنجیره جانبی، مستقیماً به استروئید ۱۹ کربنه Δ^5-3β- هیدروکسی ـ یعنی دهیدرواپی‌آندروسترون (DHEA) ـ تبدیل شود. با تشکیل Δ^4-۳-کتون، DHEA به آندروستن‌دیون تبدیل می‌گردد.

چهار واکنش لازم برای تبدیل پرگننولون و پروژسترون به محصولات ۱۷- هیدروکسیله مربوطه، با واسطه یک آنزیم منفرد به نام P450c17 صورت می‌گیرند؛ این آنزیم به شبکه اندوپلاسمی صاف اتصال داشته و توسط ژن *CYP17A1* که بر روی کروموزوم 10q24.32 قرار دارد، رمزگردانی می‌گردد. ۱۷- هیدروکسیلاز و ۲۰،۱۷- لیاز به‌طور سنتی به عنوان آنزیم‌هایی جداگانه در نظر گرفته می‌شدند. این دو کارکرد متفاوت یک آنزیم منفرد (P450c17) مربوط به امور ژنتیکی یا ساختاری نبوده، بلکه حاصل فاکتورهای اثرگذار بر تغییرات پساترجمه‌ای می‌باشد(۱۷). در مسیر تولید کورتیزول در غده فوق‌کلیه، مقدار بسیار اندکی از فعالیت ۲۰،۱۷- لیاز بیان می‌شود. در سلول‌های تکای تخمدان، سلول‌های لایدیگ بیضه و بخش مشبک[3] فوق‌کلیه، هر دو فعالیت ۱۷- هیدروکسیلاز و ۲۰،۱۷- لیاز بیان شده و مسیر استروئیدوژنز از طریق دهیدرواپی‌آندروسترون (DHEA) هدایت می‌گردد. در جسم

1- feminization
2- androstendione
3- reticularis

زرد، مسیر اصلی از طریق پروژسترون صورت می‌گیرد.

هیدروکسیله شدن پروژسترون و ۱۷α– هیدروکسی پروژسترون به واسطه‌ی پروتئین P450c21 که به ۲۱– هیدروکسیلاز هم شناخته می‌شود، انجام می‌گیرد. با شناخت خصوصیات پروتئین P450c21 و مشابه‌سازی ژنی مشخص شد که ژن ۲۱– هیدروکسیلاز *(CYP21)* بر روی کروموزوم 6p21.3 قرار دارد. یک ژن کاذب[1] غیرفعال *(CYP21P)* در مجاورت این ژن قرار دارد. بسیاری از جهش‌هایی که ژن *CYP21* را متأثر نموده و باعث هیپرپلازی مادرزادی فوق‌کلیه می‌شوند، یک سری تبدیلات ژنی هستند که حاصل نوترکیبی بین *CYP21* و جهش‌های غیرفعال‌کننده *CYP21P* می‌باشند.

آروماتیزاسیون با واسطه P450arom انجام می‌شود که در شبکه اندوپلاسمی یافت می‌شود(۱۹،۱۸). آروماتاز سیتوکروم P450 از کروموزوم 15q21.1، در جایگاهی به نام ژن *CYP19A1* (سیتوکروم P450، خانواده ۱۹ [نشان‌دهنده اکسیداسیون گروه متیل کربن ۱۹]، زیرخانواده A، پلی‌پپتید ۱) مشتق می‌شود. آروماتیزاسیون در بافت‌های مختلف و با سوبستراهای متفاوت، توسط آنزیم منفرد P450arom انجام می‌شود که توسط یک ژن واحد کد می‌گردد. نقص آروماتاز به علت جهش‌های غیرفعال‌کننده ژن *CYP19A1* بسیار نادر است؛ تعداد موارد گزارش شده، به سختی به تعداد انگشتان یک دست می‌رسد(۲۰). دختران مبتلا در بدو تولد دچار مردانه‌شدن[2] می‌گردند، زیرا جفت نمی‌تواند آندروژن‌های فوق‌کلیه جنین را به استروژن تبدیل کند؛ به این ترتیب مردانه شدن مادری نیز معمولاً در طی بارداری مشاهده می‌شود.

رونویسی آروماتاز توسط چندین جایگاه پیش‌برنده[3] تنظیم می‌شود که به سیتوکین‌ها، نوکلئوتیدهای حلقوی، گنادوتروپین‌ها، گلوکوکورتیکوئیدها و فاکتورهای رشد پاسخ می‌دهند(۲۱). بیان اختصاصی بافتی توسط پیش‌برنده‌های اختصاصی بافتی تنظیم می‌گردد. که از سویی امکان بیان شدیداً تنظیم شده آروماتاز را در تخمدان (در پاسخ به AMP حلقوی و گنادوتروپین‌ها) و بافت چربی (در پاسخ به پروستاگلاندین E_2) و از سوی دیگر بیان تنظیم نشدهٔ آروماتاز را در جفت و بافت چربی فراهم می‌آورد. یک سری مهارکننده‌های بسیار اختصاصی برای P450arom تولید شده‌اند که "مهارکننده‌های آروماتاز" خوانده شده و امکان مهار شدید تولید استروژن را فراهم می‌سازند؛ کاربردهای بالینی این مهارکننده‌ها عبارتند از: سرطان پستان (مانند آناستروزول و لتروزول) و تحریک تخمک‌گذاری.

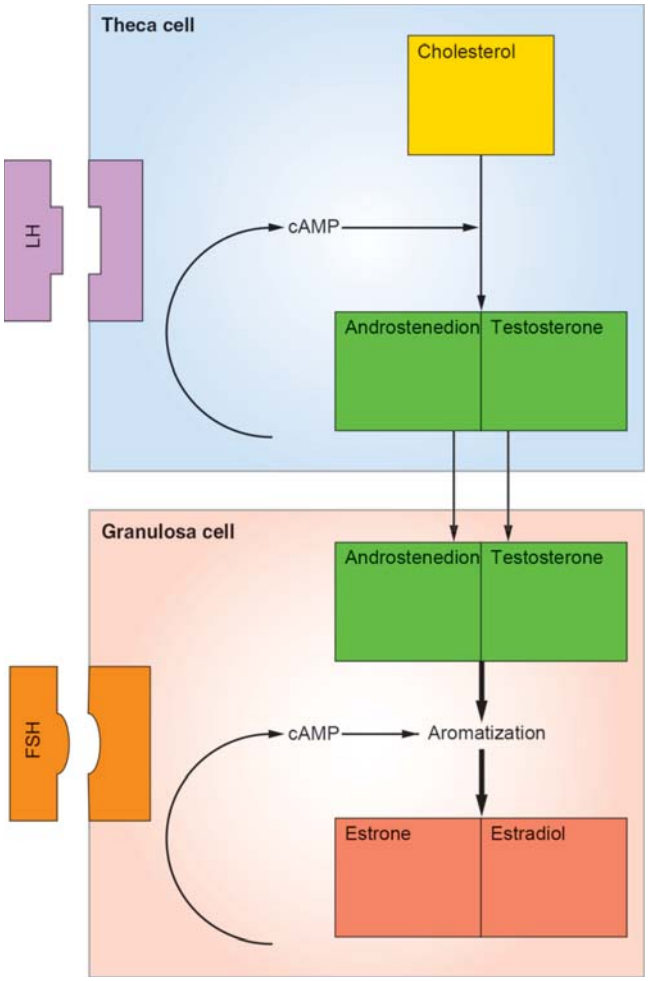
مجموعهٔ آروماتاز شامل NADPH ـ سیتوکروم P450 ردوکتاز نیز هست که نوعی فلاووپروتئین عمومی است که در واکنش‌های احیا شرکت دارد.

واکنش‌های ۱۷β– هیدروکسی‌استروئید دهیدروژناز و ۵α– ردوکتاز با واسطه آنزیم‌های غیر P450 انجام می‌شوند. ۱۷β– هیدروکسی‌استروئید دهیدروژناز به شبکهٔ اندوپلاسمی و ۵α– ردوکتاز به غشای هسته اتصال دارد. آنزیم‌های ۱۷β– هیدروکسی‌استروئید دهیدروژناز استرون را به استرادیول، آندروستن‌دیون را به تستوسترون و DHEA را به آندروستن‌دیول و بالعکس تبدیل می‌کنند. هشت ایزوزیم مختلف شناسایی و شبیه سازی شده‌اند(۲۲). آنزیم نوع ۱ در جفت و سلول‌های گرانولوزا فعال بوده و استرون را به استرادیول تبدیل می‌کند. آنزیم‌های نوع ۲ و ۴ که در بسیاری از بافت‌ها، یافت می‌شوند، آندروستندیون و استرون را به ترتیب از تستوسترون و استرادیول می‌سازند. آنزیم‌های نوع ۳ و ۵ در بیضه، آندروستندیون را به تستوسترون احیا می‌نمایند. آنزیم نوع ۶ را تنها می‌توان در جوندگان یافت. آنزیم‌های نوع ۷ و ۸ عام بوده، اما فعالیت محدودی دارند. به این ترتیب انواع ۱، ۳ و ۵، استروژن‌های فعال را از آندروژن‌ها تولید می‌کنند، حال آن که انواع ۲ و ۴، محصولات ضعیف‌تری را تولید می‌نمایند (شکلی از غیرفعال‌سازی) که به عنوان مثال در حفاظت جنین مقابل تستوسترون و استرادیول موجود در گردش خون مادر حائز اهمیت است. تولید اختصاصی سلولی هر یک از این ایزوفرم‌ها، روشی برای تنظیم غلظت موضعی استروژن‌ها و آندروژن‌ها است.

استروژن‌ها

آندروژن‌ها پیش‌ساز استروژن‌ها می‌باشند. آندروستن‌دیون طی فعالیت ۱۷β– هیدروکسی‌استروئید دهیدروژناز به تستوسترون تبدیل می‌شود. تستوسترون، محصول ترشحی اصلی تخمدان طبیعی به شمار نمی‌رود. تستوسترون به سرعت در موقعیت کربن ۱۹ دمتیله شده و متعاقب آروماتیزاسیون به استرادیول تبدیل می‌گردد؛ استرادیول، استروژن ترشحی اصلی تخمدان

1- pseudogene
2- virilization
3- promoter



شکل ۶-۱

انسان می‌باشد. این مراحل شامل سیستم شناخته شده «دو سلولی» می‌شدند که به‌طور کامل در فصل ۵ مورد بحث قرار گرفته است **(شکل ۶-۱)**. استرادیول تا حد زیادی از آندروستن‌دیون (از طریق استرون) حاصل می‌شود. خود استرون نیز روزانه به مقادیر قابل‌توجهی ترشح می‌گردد. استریول، متابولیت محیطی استرون و استرادیول بوده و فرآورده ترشحی تخمدان نمی‌باشد. تولید استریول، شاخصه "سمیّت‌زدایی" متابولیک عمومی (تبدیل مواد فعال از نظر زیستی به اشکال کمتر فعال) می‌باشد **(شکل ۷-۱)**.

تبدیل استروئیدها در بافت‌های محیطی همواره شکلی از غیرفعال‌سازی نیست. آندروژن‌های آزاد در بافت‌های محیطی (به عنوان مثال در پوست و سلول‌های چربی) تبدیل به استروژن‌های آزاد می‌شوند. جایگاه سلول‌های چربی بر فعالیت این سلول‌ها تأثیر می‌گذارد. زنان مبتلا به چاقی مرکزی آندروژن‌های بیشتری تولید می‌کنند(۲۳). تحقیقات سیتری و مک‌دونالد(۲۴) نشان داد میزان آندروژن موجود در گردش خون برای تولید استروژن کافی جهت ایجاد خونریزی در زنان یائسه کافی است. در زنان، غده فوق‌کلیه به عنوان منبع اصلی تولید

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Chapter four

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Chapter five

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Chapter six

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Chapter seven

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Chapter eight

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Chapter nine

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Chapter ten

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Chapter eleven

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Chapter twelve

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Chapter thirteen

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Chapter fourteen

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Chapter fifteen

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Chapter sixteen

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